THE UNIVERSITY OF ALBERTA

REPRODUCTION OF THE NORTHERN PINTAIL IN ALBERTA: FEMALE TRAITS AND NEONATE BODY RESERVES

by

DAVID CRAIG DUNCAN

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Abstract

Nest-site placement of Northern Pintails (*Anas acuta*) was examined on the prairie of southern Alberta. Northern Pintails nested on the grazed mixed prairie around shallow waterbodies in greater numbers than any other duck species. Nests were commonly placed 1-3 km from water. The hypothesis that nesting far from water is a result of male chasing was rejected in favor of a predator avoidance hypothesis. Nest-to-water movements by ducklings did not deplete their lipid reserves and did not appear to be physiologically detrimental. Overland travel may not be as hazardous as generally assumed.

Captive Northern Pintails nested earlier, laid larger clutches, and renested more readily than did wild birds in southern Alberta. Food may limit these parameters in the wild. Wild adults nested earlier and laid larger clutches, independent of the laying date, than did yearlings. The reproductive output of Northern Pintails nesting in southern Alberta was considerably lower than that of birds breeding at Delta, Manitoba, and appears low compared to other dabbling ducks.

Clutch size was strongly correlated with laying date. A number of proximate causes including hen age, renesting, and poor food supply suggested to explain this phenomenon are rejected. It appears that laying date itself is the influencing factor although the exact mechanism is unknown. The ultimate reason for this seasonal decline in clutch size may be a seasonally declining survival rate of the young which has selected for reduced reproductive effort later in the breeding season.

The egg size of Northern Pintails was quite variable, but no more so than morphological features of hens. Egg size was a good predictor of size of the young. Diet can have a strong influence on egg size. A number of other sources of potential variation in egg size were examined and found to have little or no effect. Individuals consistently laid similar sized eggs. There was no significant heritability value for egg size between captive daughters and wild mothers. The utility of heritability values to ecologists is discussed.

Neonate Northern Pintails were found to have a high lipid content primarily attributable to their large carcass fat deposits. These carcass reserves were the most important source of energy under starvation conditions. The yolk was important to growth of the ducklings but was not an important source of nutriment to starving ducklings.

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I. INTRODUCTION

ACADEMIC RATIONALE

Why study reproductive traits and neonate body reserves? Natural selection is based on survival of the "fittest" and because of the difficulty in assessing lifetime fitness of iteroparous organisms in the wild, seasonal reproductive output is often used as a measure of fitness. Both reproductive parameters and neonate body reserves are believed to be closely linked to the reproductive success of an individual. The knowledge of fitness traits and the variation within them enables us to better understand how natural selection has shaped the organisms that we observe today. This is what evolutionary ecology attempts to comprehend and why a study of reproductive traits may be deemed "important".

The above is typical, though perhaps shorter than, what one might expect in a thesis introduction entitled "Rationale". What is considered to be the rationale, or reason(s), for a study is subjective, dependent upon the outlook of the person inquiring. What constitutes bona fide rationale in the opinion of one may not be acceptable to another because rationales are often not scientific truths but rather philosophical beliefs.

On the broadest level, the reason for my study is the same as that for research in general; it created new knowledge. Bonneau and Corry (1972) argued that the quest for new knowledge "...is justified on cultural grounds, enlarging and exalting the spirit somewhat as music, art and literature do" (p.43), and that a central element of West European cultural tradition "...is the value of truth as something indispensable to humanity, and the obligation felt to pursue it, declare it, and sustain it" (p.16). The generation of new knowledge has also been rationalized on the basis that "the nature of man demands that he continue to explore, and that, generation after generation, he seek to learn more about the universe and about himself. Research for its own sake is one of the noblest activities of man and one of the ways of enriching life" (Macdonald et al. 1969: 7). Research contributes "...to the conceptual development of science. This is to say, the motivation is to add to the accumulated, objective and systematic knowledge of the inherent properties and interactions of matter, space, energy, natural phenomena and biosystems" (Science Council of Canada 1972: 18). Research has been justified because it can "...improve the health and longevity of Canadians, enrich our cultural resources, (and) improve the quality of the environment in which we live..." (Macdonald et al. 1969: 2). One of the subobjectives of the Natural Sciences and Engineering Research Council of Canada (NSERC), which provided much of the funding for this study, is "...to support excellence in research for the creation of new knowledge" (NSERC 1985: 1). Thus, my study can be rationalized, as can research in general, on the basis that it produced new knowledge.

Another line of justification for my research is that it provided me with the opportunity to learn how to conduct research. The opportunity to conduct research is necessary to develop teachers and students, and to produce good scientists (Science Council of Canada 1972). Research is valuable because it enhances "...individual intellectual opportunity..." (Macdonald et al. 1969: 2). Another NSERC subobjective is "...to assist in the provision and development of highly qualified manpower" (NSERC 1985: 1). Consequently, my research can be justified on the basis that it was an educational experience that permitted me to learn about zoology and how to do research.

Both of the above rationalizations are those given for pure or basic research in general. Some types of research can also be justified because they are applied or practical. My study received support from the Canadian National Sportsman's Fund and Ducks Unlimited (Canada). The reasons for their support were undoubtedly based on the fact that my study was concerned with ecological aspects of an important game species and that ultimately, my research would be useful for the management and conservation of that species. Thus, another reason for my research was that it was concerned with matters of a desirable wildlife species that could have practical benefits for its future management.

Science is the systematic search for truth or facts. The above rationalizations were made *a posteriori* and may not constitute "good science". From my perspective, the following were some of the proximate facts or truths of why this study was conducted and thus constitute "good science" as a rationale.

The answer to the question why study a bird, or why study a duck, is simply because I wanted to: personal interest. I chose to study the Northern Pintail (*Anas acuta*) because it was practical, it being the most abundant duck species on my study area. As I read more about this species and observed it more, I gained a keen interest in it. The Northern Pintail was also personally attractive as a study animal because it is an important game species and, thus, the study would have practical importance.

The primary reasons for studying reproductive traits were: 1) intellectual curiosity; I was interested and these things were unknown, and 2)potential practical benefits; some aspects could be useful to biologists and managers. Another reason for this study was the experience I gained when initially starting a Master of Science research project on duck brood survival. The observations I made and the data I collected in that first field season made me inquisitive about those subjects that have come to constitute my dissertation. Some of the contents of this thesis are attributable to the interest and guidance of my supervisor and supervisory committee. Hence, those persons were the reason for conducting some aspects of this research and they deserve some of the credit (or blame). I also justify my research on the basis that it was concerned with what I perceived to be biologically important questions. Reproductive traits such as laying date, clutch size, and egg size are closely related to fitness and are, in my opinion, very basic characteristics of species, deserving of study.

STUDY ANIMAL

The Northern Pintail is a holarctic species and is the second or third most abundant duck in North America (Bellrose 1976). It breeds in most parts of the northern half of continental North America although it is an uncommon breeder in the eastern half of the continent and, on the west coast, nests as far south as California (Bellrose 1976, Palmer 1976). Northern Pintails typically nest in treeless areas and, during the breeding season, are most abundant on the mid-continent prairies and in parts of Alaska (Bellrose 1979). The birds migrate to the southern United States and northern Mexico for the winter. Two behavioral characteristics of the Northern Pintail that set it apart as an anomaly among ducks are: 1) its lack of territorial behavior during the breeding season combined with a high level of sexually-oriented pursuit of females by males (Smith 1968, Derrickson 1978, Titman and Seymour 1981), and 2) its pronounced movement to northern areas during the breeding season when droughts occur on the prairies (Smith 1970, Derksen and Eldridge 1980).

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II. NEST-SITE SELECTION BY NORTHERN PINTAILS ON THE PRAIRIE OF ALBERTA: CAUSATION AND CONSEQUENCES FOR DUCKLING SURVIVAL

INTRODUCTION

Northern Pintails (*Anas acuta*) typically breed in open, treeless areas (Hilden 1964, Bellrose 1976); during the breeding season in North America they are most numerous on the mid-continent prairie, particularly southern Alberta and Saskatchewan, and on parts of the arctic tundra, principally in Alaska (Bellrose 1976, 1979). Although some arctic areas are inhabited by large numbers of Northern Pintails during drought years on the prairie, the reproductive output of these birds appears to be low (Calverley and Boag 1977, Derksen and Eldridge 1980). The importance of the prairie breeding habitat to the overall productivity of Northern Pintails is evidenced by the positive correlation between continental recruitment and the relative proportion of birds inhabiting the prairies (Smith 1970).

The prairies of southern Alberta support higher densities of breeding Northern Pintails than any other region (Vermeer 1972, Bellrose 1979). Much of this area is rangeland and consequently many of the birds breeding there nest on grazed prairie. Most information available to date on the location of nest-sites of Northern Pintails has come from Manitoba and North Dakota where Northern Pintails are frequently found nesting, often unsuccessfully, in cultivated fields (Sowls 1955, Milonski 1958, Higgins 1977, Krapu 1977).

This study examines the location of Northern Pintail nests around a number of shallow basins in grazed prairie near Brooks, Alberta. The use of artificial islands for nesting sites is compared to that of the mainland including the location of nests of other duck species. The distance of Northern Pintail nests from water is determined and the hypothesis that male pursuit flights causes hens to nest far from water is considered. The consequences of nesting far from water on the subsequent survival of Northern Pintail ducklings is also examined.

STUDY AREA AND METHODS

The study was conducted in an area of grazed mixed grass prairie about 35 km south-east of Brooks, Alberta from 1981-1984. The study area included four impoundments which are managed for waterfowl production by Ducks Unlimited Canada. These impoundments (Tilley O, Tilley P, Kininvie F, and Kininvie S) are described by Giroux (1981). At high water levels, the areas of these impoundments were, respectively, about 0.7, 0.2, 2.0 and 0.75 km². Each basin contained artificial islands. The water in these impoundments was less than 1 m deep except for 1-2 m deep moats around the islands.

The mainland vegetation was mixed prairie of the *Stipa-Bouteloua* association (Coupland 1961), although the short grass, blue grama (*Bouteloua gracilis*), predominated in this area. Scattered clumps of silver sagebrush (*Artemisia cana*) and plains pricklypear (*Opuntia polyacantha*) were the most conspicuous components of the vegetation. Fringed sagebrush (*A. frigida*), spikemoss selaginella (*Selaginella densa*), moss phlox (*Phlox hoodii*), and ground-dwelling lichens are common. The shorelines of the waterbodies consisted of a small (<10 m) zone of relatively dense mid-height grasses. The mainland vegetation remained essentially unchanged throughout the summer, whereas there was extensive growth on the artificial islands. By early summer, the built-up islands were about half-covered with 0.5- to 1-m-high forbs such as Canada thistle (*Cirsium arvense*), bull thistle (*C. hookerianum*), lambsquarters goosefoot (*Chenopodium album*), flixweed tansymustard (*Descurainia sophia*), and common Russianthistle (*Salsola kali*). Sparse mid-height grasses and bare earth covered the other half.

Nest searches were conducted on the islands and mainland every 3 weeks or less. The artificial islands were searched by walking across them systematically whereas the mainland was searched by flushing hens from nests with a 50-80 m steel rope dragged between two vehicles along parallel transects. Duck nests were attributed to a species based on identification of the flushing hen, and occasionally by characteristics of the eggs and feathers in the nest. The stage of incubation of the eggs was estimated by candling, using Weller's (1956) guide to embryo development. Laying date was calculated by back-dating from the stage of incubation and size of the clutch. To obtain data on individual Northern Pintails, hens were trapped on their nests using drop traps (Sowls 1949), modified Weller traps (Weller 1957), or bow-net traps (Sayler 1962a), and identified as either yearlings or adults based on wing-feather characteristics (Duncan 1985a). The straight line distance from a nest to water was measured by vehicle odometer.

The comparison of island- and mainland-nesting ducks was restricted to Kininvie F because the southern perimeter of this impoundment was the site of the principal mainland study plot. In 1982, the mainland around the southern perimeter of Kininvie F was searched out to about 500 m from shore. The study plot covered 1.65 km^2 and included a small amount of grassy shoreline. In 1983 and 1984, nest searches were conducted along parallel transects that were perpendicular to the shoreline and were extended out to 1.5 km and 3.0 km from the shore, respectively. In the latter 2 years, nest searches were restricted to prairie vegetation and did not include any shoreline vegetation. The area searched during 1983 was about 4.0 km^2. In 1984 only a limited amount of nest searching was conducted on the mainland and species other than Northern Pintail were ignored to expedite the searches. Each year, all 14 artificial islands in Kininvie F were searched for nests. The average dimensions of the islands determined by tape measure was 18 x 51 m for a total area of 1.33 ha.

To examine the effect of a long nest-to-water movement on newly-hatched Northern Pintails, ducklings from artificially-hatched clutches were walked 3 km outdoors when 12-24 h old [ducklings generally remain in the nest for 12-24 h after hatch (Kear 1965, Bjarvall 1968)]. Half of each brood was randomly selected to be walked with the remainder of the brood being maintained outdoors in a 1-m-diameter enclosure. The walked ducklings were led by a human at the speed of 1 km/h (see Duncan 1983). At the half-way point, the ducklings were permitted to rest for about 5 min if they appeared tired. After the walk, the entire brood was placed together in a 1-m-diameter indoor brooding facility with heat lamps and free access to water. Only synchronously-hatching broods were used.

Some broods were given ad libitum food (22% protein goose and duck starter, Lakeside Feeders Ltd.) after the walking experiment and their growth was monitored by weighing the ducklings and measuring their culmens and tarsometatarsi. Measurements were taken after the walk and at subsequent 2 day intervals up to 11 days of age. The culmen was measured between the distal tip and proximal median of the upper mandible, and the measurement of the tarsometatarsus included the distal condyle of the tibiotarsus. Measurements were made with vernier calipers.

Some broods were prohibited access to food after the walking experiment and were sacrificed 24 h after the end of the walk to examine their energy reserves. Yolk sacs and livers were excised and weighed and the remaining body was frozen for subsequent lipid extraction. Lipid analysis of the carcass (without feathers, bill, feet, yolk sac, and liver) was conducted with petroleum ether in a Soxhlet apparatus.

Statistical analyses were conducted using the SPSSX package with a significance level of 0.05. Repeatabilities were calculated as outlined by Falconer (1960).

RESULTS AND DISCUSSION

Northern Pintails were the predominant duck species nesting on the mainland prairie, their nests comprising 53-67% of all mainland duck nests (Table II-1). The higher proportion of Northern Pintail nests in the 1983 searches was likely a result of: 1) searching further from water where Northern Pintails were relatively more prevalent, 2) the omission of the grassy shoreline which contained a number of nests of other duck species [particularly Blue-winged Teal (*A. discors*)], and 3) an apparent decrease in numbers of nesting Green-winged Teal (*A. crecca*). The next most common species nesting on the mainland prairie were Northern Shovelers (*A. clypeata*), Blue-winged Teal, and Green-winged Teal. Similarly, Keith (1961) found that Northern Shovelers, Blue-winged Teal, and Northern Pintails were the main duck species nesting on an area of mixed prairie about 100 km from that studied here.

Table II-1. Species composition in percent (*n* in parentheses), and density of duck nests on mainland and artificial islands, Kininvie F, Alberta.

	Mainland		Artificial islands
Species	1982[a]	1983[b]	(1981-1984)
Northern Pintail	53 (27)	67 (70)	13 (57)
Northern Shoveler	8 (4)	20 (21)	2 (9)
Blue-winged Teal	14 (7)	4 (4)	5 (23)
Green-winged Teal	10 (5)	1 (1)	1 (2)
Gadwall	6 (3)	1 (1)	25 (104)
Mallard	4 (2)	0 (0)	24 (102)
Lesser Scaup	2 (1)	0 (0)	21 (87)
American Wigeon	0 (0)	4 (4)	2 (7)
Redhead	0 (0)	0 (0)	2 (10)
Ruddy Duck	0 (0)	0 (0)	1 (2)
Unknown	4 (2)	3 (3)	5 (22)
Total	101 (51)	100 (104)	99 (425)
Density (nests/ha)	0.31	0.26	80.0

[a] Includes small amount of grassy shoreline; searched to 500 m from water.

[b] Only prairie vegetation; searched to 1600 m from water.

In contrast to the species composition of ducks nesting on the mainland, Gadwalls (*A. strepera*), Mallards (*A. platyrhynchos*), and Lesser Scaup (*Aythya affinis*) were the prevalent species on the artificial islands. This was primarily because of their greater propensity for nesting in the dense forb cover on the islands (Duncan 1986a). Gadwalls, Mallards, and Lesser Scaup often nest in high densities on islands (Giroux 1981). Giroux (1981) studied a number of shallow impoundments in the same area as this study, including Kininvie F, and found that Northern Pintails and teal comprised a higher proportion and Gadwall and Lesser Scaup a lower proportion of the island-nesting ducks than in this study. These differences could be attributed to the fact that the single waterbody considered herein, Kininvie F, is the most permanent of the shallow waterbodies studied by Giroux (1981) and thus might receive heavier use by late-nesting species such as Gadwall and Lesser Scaup. Other possible reasons could be increased vegetative cover through succession over the intervening years, thus attracting more Gadwall and Lesser Scaup, and/or differential species recruitment since Giroux's (1981) study.

The density of duck nests on the artificial islands was much greater than on the mainland (Table II-1). The nest density of Northern Pintails was higher on the artificial islands (10.4 nests/ha) than on the mainland (0.16-0.17 nests/ha), as was that of every other species, although the "preference" of Northern Pintails for islands was weak compared to that of Gadwalls, Mallards, and Lesser Scaup. Because each species nested in higher density on the islands than on the mainland suggests an overall "preference" for insular habitats and/or increased success and survival of island-nesting hens and subsequent increased homing and recruitment to islands. Giroux (1981) found that the nest density on these same islands averaged only 29/ha compared to the 80/ha found herein. This difference is likely attributable to lower water levels during Giroux's study and the inclusion of island berms in his calculation of island area (Giroux pers. comm.). During my study, the berms were seldom exposed and when a few were, it was after ducks had finished nesting. Other minor effects that could have contributed to the increase in density might be increased recruitment over the succeeding years by those species which commonly nest in higher densities (see above), and erosion of the area of the islands. When Giroux (1981) studied these islands, the nest density he reported was low compared to other island studies and he suggested that this might have resulted from the high densities of islands in the impoundments he studied and subsequent differential island use. The nest densities I found were higher than that reported from most other islands (see Giroux 1981), and thus the above hypothesis appears unwarranted.

The mainland nest densities of all species combined (0.26-0.31/ha) were virtually identical to the 0.29 nests/ha that Keith (1961) reported from another area of mixed prairie in southern Alberta. Mixed prairie does not provide the cover that is sought out by densely-nesting species such as Gadwall, Mallard, and Lesser Scaup, and consequently has a lower density of duck nests than do areas with more rank vegetative cover (Duebbert and Lokemoen 1976, Duebbert 1982, Duncan 1986a). The higher nest density on the mainland in 1982 compared to 1983 is attributable to a small concentration of nests in the grassy shoreline included in the 1982 searches and to the shorter distance from water over which the 1982 searches were conducted [most species nest close to water (Bellrose 1976)].

The preponderance of Northern Pintail nests on the mainland prairie reflects the Northern Pintail's habit of nesting in very sparse cover (Keith 1961, Kalmbach 1938, Munro 1944, Stoudt 1971, Sowls 1955). Their somewhat misdirected selection of cultivated fields as nesting sites [the nest is often destroyed because of agricultural activity (Milonski 1958, Krapu 1977)] likely results from their preference for physiognomically open areas, illustrating their adaptation to nesting in sparsely-vegetated prairie. Although many Northern Pintail nests that I found on the prairie were situated beside a small clump of silver sagebrush, they had essentially 0% cover from above and only 10-40% cover on the sides. Numerous other nests were situated on the open prairie with no cover. Because there was a profusion of silver sagebrush clumps that were not used as nesting sites and a low density of nests, nesting by Northern Pintails in completely exposed sites on the open prairie was by choice. Many nests, particularly those with no cover, were located in natural depressions in the ground. The dull coloration of the bill and speculum of Northern Pintail hens may add to the bird's crypticity and be adaptations for nesting in open sites. A few Northern Pintails initiated nests relatively late in the breeding season on the islands and consequently their nests were in dense forb cover. During a coincidental study of reproduction in captive Northern Pintails, I found that many hens nested in the secluded nesting sites provided (100% overhead and 80% lateral cover). This behavior was likely caused by human activity and appears to illustrate that the tendency for Northern Pintails to select nest-sites in sparse cover can be affected by environmental conditions.

I recorded Northern Pintails nesting as far as 3 km from water and found no tendency for hens to concentrate their nests close to water although the number of nests 2-3 km from water appears to be relatively low (Fig. II-1). The distribution of nests depicted in Fig. II-1 is based upon equal areas searched at the various distances from water and thus represents relative densities. Because the total area at a given distance from a waterbody is greater than that closer to water, the fairly similar nest densities within 1 km of water (Fig. II-1) mean that the actual number of nests at 1 km would be greater than that close to shore. Using the

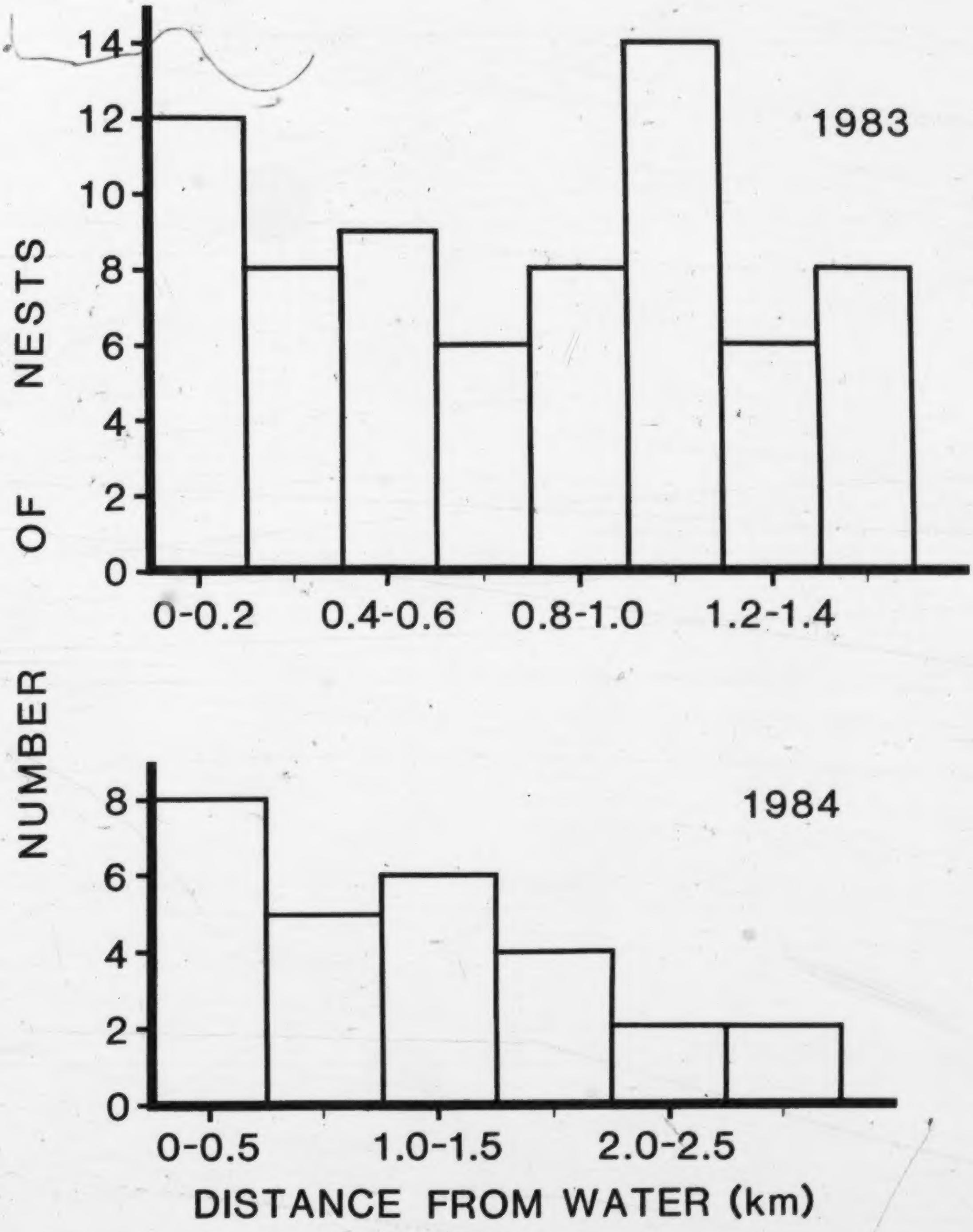

Fig.II-1. Frequency distribution of distance of Northern Pintail nests from water, based on equal areas searched at all distances from water.

data from Fig. II-1, a theoretical distribution of the number of nests around a 1-km-diameter circular waterbody were calculated (Fig. II-2). These show that the largest number of hens nest 1-2 km from water and that there are as many hens 2-3 km from water as there are 0-1 km. Thus, unweighted mean nest distances from water calculated from the data in Fig. II-1 may substantially underestimate the true mean. With this in mind, the unweighted mean distance of Northern Pintail nests from water in 1983 was 781 ± 56 m (*n* = 71) and in 1984 was 1126 ± 170 m (*n* = 27). Some Northern Shovelers were also found nesting far from water; a number of their nests were as far as 1.4-1.5 km from water. At the opposite extreme, Lesser Scaup exhibited a strong tendency to nest near water on the mainland, with Blue-winged Teal being the next most hydrophilic upland-nesting species. Duck nests have occasionally been recorded 2.0-2.5 km from water (Sayler 1962b, Dzubin and Gollop 1972) although most dabbling ducks appear to nest within 100 m of water (Bellrose 1976). Northern Pintails often nest farther from water than other duck species (Bent 1923, Bengston 1970, Keith 1961) although previously reported mean distances of nests from water are much smaller than recorded herein, ranging from only 50 m (Keith 1961) to 190 m (Derrickson 1977). A few Northern Pintail nests have been found over 1.5 km from water (Sowls 1955, Bellrose 1976). The low mean distances reported by others are primarily a result of nest searches being conducted closer

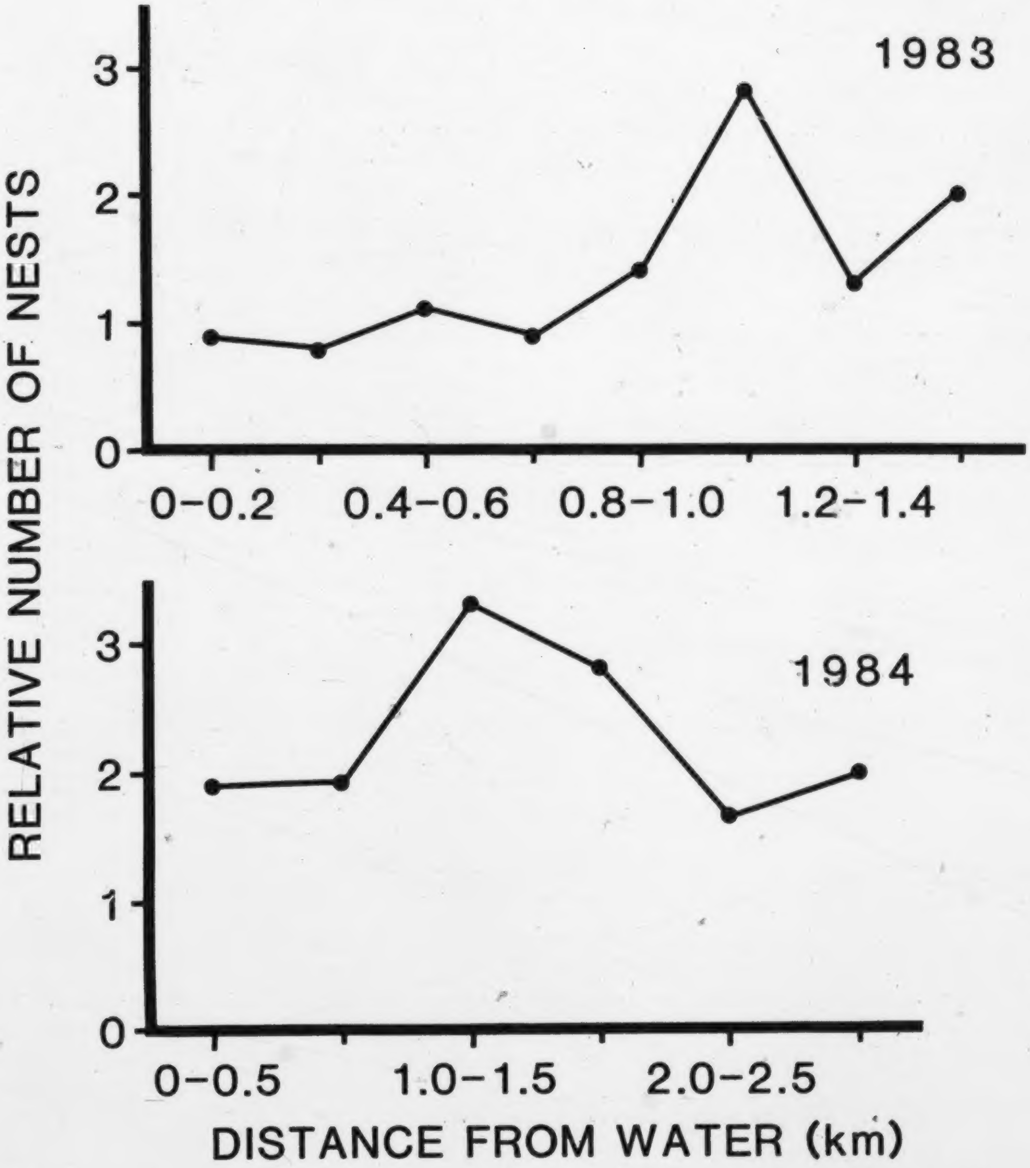

Fig.II-2. Theoretical distribution of relative number of Northern Pintail nests at different distances from water around a circular 1-km-diameter waterbody, based on data from Fig.II-1.

to water [eg. Keith (1961) only searched 274 m from water]. Because the entire upland in my study was mixed prairie, there was no confounding influence of varying vegetative types at different distances from water, and thus the nest-sites reported herein reflect only selection of distance from water. Potential limiting factors on the maximum distance of Northern Pintail nests from water are lack of additional increase in nesting success at greater distances, increased probability of duckling mortality, and increased flight costs to the hen during incubation recesses (see Ringelman et al. 1982).

There were no differences in nest-site placement between yearling and adult Northern Pintails. Both age classes nested at similar distances from water (1982-1984 combined, adult $\bar{x}$ = 722 ± 67 m, *n* = 85, yearling $\bar{x}$ = 661 ± 140, *n* = 26, t = 0.43, NS) and the same proportions of adults and yearlings nested on the artificial islands and the mainland (1982-1984 combined, *n* on island/mainland, adults = 43/108, yearlings = 13/43, Chi-square = 0.34, NS). Thus, there was no evidence for displacement of younger birds into suboptimal habitat as Dzubin (1969) suggested might occur in Mallards.

Smith (1968) thought that sexual pursuit flights by drake Northern Pintails caused pairs to disperse and subsequently resulted in dispersion of nests. McKinney (1965) considered that such behavior might ultimately be adaptive because the increased distance between nests could result in a decreased probability of predation. Although McKinney (1965) viewed nest dispersion in most ducks as an indirect result of pair dispersion, he thought it likely that male chasing in Northern Pintails caused females to nest at a considerable distance from water (McKinney 1973). Unlike most other ducks, Northern Pintails are not territorial and males show little hostility towards conspecific males but engage in a high degree of sexually-oriented pursuit of females (Smith 1968, Derrickson 1978, Titman and Seymour 1981). If male chasing actively disperses nesting hens, Northern Pintails should nest closer to water when there is a paucity or absence of males and nests initiated late in the breeding season after most males have left would be expected to be situated closer to water. However, nest placement in relation to distance from water was not a seasonally dynamic phenomenon as nest distance from water was not correlated with laying date (in 1983, the only year with substantial sample size, $r = -0.13$, $n = 70$, NS). In addition, in the drought year of 1984, the number of breeding birds was low (only 2 Northern Pintail nests were initiated on the islands compared to a mean of 19 in 1981-1983) yet hens continued to nest far from water (Fig. II-1). Because males appeared to confine most of their chasing activity to areas near or over water, it is improbable that males actively forced hens to nest as far as 3 km from water. The much higher density of nesting hens on the islands compared to the mainland is also contrary to the male pursuit hypothesis. A final point against the hypothesis that male pursuit causes hens to nest far from water is that hens exhibited nest-site fidelity; they tended to nest near the site of their previous year's nest as has been shown in other ducks (McKinney 1965) showing that nest placement is influenced by previous experience or some inherent tendency. Female Northern Pintails exhibited a high degree of consistency in the distance they nested from water, shown by a 0.87 repeatability value for 15 recaptured hens [repeatabilities range between 0-1 and represent relative importance of among individual variance (Falconer 1960)]. Seven of these females were recaptured nesting on the same small artificial island; the islands averaged 51 x 18 m and were 100-200 m apart. Two females that were found nesting on an island in one year and on the mainland in another, nested close to the shore (< 50 m) on the mainland. The 6 females that nested only on the mainland had a moderate repeatability of 0.51 for the distance they nested from water. Thus, nest-site selection by Northern Pintail hens does not appear to be an active, dynamic process dependent upon male pursuit flights. There may be some passive component of intraspecific avoidance of males by females as I observed a few hens exhibiting avoidance behavior of males similar to that observed by Derrickson (1977). This might contribute to nest dispersion but only when a hen which is in the process of selecting a nest-site observes a male other than her mate. It is unlikely that such avoidance behavior is responsible for the placement of numerous nests 1-3 km from water.

The idea that hens are actively "forced" to nest far from water probably originates from the assumption that the required overland travel by broods from nest to water substantially reduces duckling survival (eg. Sayler 1962b, Bengston 1970, Dzubin and Gollop 1972, Ball et al. 1975). In Northern Pintails, any cost of nesting far from water must be less than the benefit of doing so because many hens do nest considerable distance from water. Such behavior can only persist if it is selectively advantageous overall (Eriksson 1978).

Overland movements by duck broods, particularly Northern Pintails, may not be as hazardous as commonly assumed. Northern Pintails broods are known to be very mobile (Evans et al. 1952, Diem and Lu 1960, Duncan 1983) and the nest placement reported herein shows that most Northern Pintail broods must walk over 1 km to get from their nest to water. Although duckling loss during overland movement is usually no more than an assumption, Ball et al. (1975) found a negative correlation between distance traveled overland by young ducklings and the number of surviving ducklings. However, cause and effect cannot be discerned in the analysis, and the relationship was weak, explaining only 15% of the total variation. Other studies have found no relationship between duckling survival and overland travel (Evans et al. 1952, Talent et al. 1983) and recent studies of duck brood survival have shown that most mortality occurs on water not on land (Talent et al. op cit, Duncan 1985b). Duck broods can and do undertake lengthy overland movements (eg. Wright 1954, Berg 1956, Evans and Black 1956, Mendall 1958, Stewart 1958, Young 1967, Dzubin and Gollop 1972, Alison 1976, Duncan 1983), and although there is some risk to duckling survival, the magnitude is unknown and is likely much lower than has previously been assumed.

Overland brood movements could be less hazardous to ducklings on the open prairie than in areas with more dense vegetation. Open terrain might be advantageous to hens and broods if it enables improved detection of predators and easier movement by ducklings which could decrease the probability of predatory and accidental loss of ducklings. The major presumed danger to ducklings during overland walks is often considered to be an increased probability of predation (eg. Leopold 1951, Wright 1954, Alison 1976). Movement over open prairie could be disadvantageous because ducks may be more easily sighted by predators and might be more susceptible to avian predation. Although I observed instances of unsuccessful hawk attacks on a Northern Pintail brood moving overland (Duncan 1983), a hawk was suspected as the cause of loss of another brood walking from nest to water (Duncan 1985b). I also observed California Gulls (*Larus californicus*) attacking duck broods but only on the water. It appeared that gulls may have better success when a brood is on water rather than land because on water, ducklings may dive and get separated from the hen and be more vulnerable to attack.

I suggest that Northern Pintail hens nest far from water by "choice" because it ultimately decreases the chance of their clutch being depredated as their nests are farther from the activity centers of most nest predators. Because Northern Pintails nest in sparse cover, they may be relatively vulnerable to predators and consequently there may be greater selective pressure on them to nest further from water than those species that nest in denser cover. The principle nest predator in my study, the Striped Skunk (*Mephitis mephitis*), may concentrate its activity close to areas where there is more cover, such as shorelines (Milonski 1958, Keith 1961). Anderson (1981) found that natal (maternal) dens of Striped Skunks on the mixed prairie were always close to cover and water. I observed Striped Skunks most frequently near water or cover although one Striped Skunk destroyed nests on the prairie about 1 km from water. Keith (1961) suggested that higher soil moisture close to water might enhance odors and increase a mammalian predator's ability to locate a nest, however, this is not a tenable explanation for the placement of Northern Pintail nests 3 km from water on xeric prairie. I observed California Gulls and Ring-billed Gulls (*Larus delawarensis*) eating duck eggs and although their activity was centered around waterbodies, they were frequently observed flying over the prairie and appeared to be searching for food items. The hypothesis that Northern Pintails nest far from water to avoid nest predators predicts that hatching success of nests is reduced closer to water. Some studies have found higher predation rates on nests that are closer to water (Livezey 1981, Page and Cassel 1971). Keith (1961) found reduced nest predation further from water in some moist, dense vegetation types but not in other habitats including mixed prairie. Cowardin et al. (1985), however, found that successful Mallard nests were on average closer to water than were unsuccessful ones. The differences between these studies may result from a confounding effect of different vegetative cover types at different distances from water.

Hatching success of nests on the mainland appeared to be fairly high although various levels of predator control were conducted during most of this study. In 1981, predator control efforts were minimal and the hatching success of Northern Pintail nests on the mainland was 64% (*n* = 33) as determined by the Mayfield method (Miller and Johnson 1978). Because Northern Pintails nest in such low densities and at considerable distance from water over large tracts of prairie, the probability of a predator locating a nest is likely much lower than in intensively farmed areas where duck nests of various species tend to be concentrated in small strips of cover through which a predator can efficiently search. The hatching success of Northern Pintail nests on islands in 1981 was 44% (*n* = 27), lower than that on the mainland. Gulls were suspected as the primary cause of clutch loss on the islands. Dense nesting concentrations of Northern Pintails on islands may be prevented by their habit of nesting in sparse cover which would predispose them to avian predation and by an inherent tendency to nest away from water.

To examine the effect of a long nest-to-water walk on the energy reserves of Northern Pintail ducklings, recently-hatched ducklings were walked 3 km and their energy depots were examined 24 h thereafter. Walked ducklings did not differ from the unwalked ducklings in size of yolk sac or liver, or in absolute and relative carcass lipid content (Table II-2). There was, however, a significant walk-brood interaction in the analysis of yolk sacs suggesting that some variable in the experimental design affected the results of the walk (eg. temperature) or that the broods differed in their response to walking. Lack (1967) speculated that the large fat stores of neonate ducklings enabled them to walk considerable distance from their nest-site to water. Krapu (1974) thought that this might be particularly important in Northern Pintails because they often nest far from water. The results reported herein show that a 3 km overland walk did not cause any appreciable assimilation of lipid stores in Northern Pintail ducklings. Krapu (1979) also suggested that nutrient reserves in the yolk might be important for overland movement, however, my results show that the yolk mass of walked ducklings

Table II-2. Effects of a 3 km overland movement on energy depots of 12-24 h old Northern Pintail ducklings (mean ± SE). Half of each brood (n = 6) was walked, and birds were sacrificed 24 h after the walk.

		Carcass[a]			
Group	n	Lipids (g)	Lipid index[b]	Yolk sac (g)	Liver (g)
Walked	20	0.89 ± 0.09	0.29 ± 0.03	0.24 ± 0.05	1.05 ± 0.04
Unwalked	18	0.84 ± 0.10	0.28 ± 0.03	0.36 ± 0.06	1.03 ± 0.04
Difference[c]		NS	NS	NS[d]	NS

[a] Carcass of duckling minus feathers, bill, feet, yolk sac, and liver.

[b] Index = g lipid/ g lean dry mass.

[c] Two-way anova with broods as random effect; NS = not significant ($P > 0.20$).

[d] Significant brood-walk interaction ($P = 0.03$).

generally did not different from that of unwalked ducklings (Table II-2). Overall, a 3 km nest-to-water walk was not physiologically detrimental to newly-hatched Northern Pintail ducklings at the gross quantitative level examined in this study. Because most of a duckling's energy reserves are in its carcass lipids (Duncan 1986b), the lack of a difference in carcass lipids between walked and unwalked ducklings shows that 3 km nest-to-water movements are not energetically costly. The 3 km walks were, however, visibly tiring for the ducklings; walked ducklings often slept immediately after the walk whereas the control birds did not. Undoubtedly there was some minor effect on the energy stores of the walked ducklings, possibly a reduction in glycogen reserves resulting from increased anoxic stress and glycolysis. Because glycogen stores are used to withstand anoxic stress, Freeman (1965) suggested that glycogen stores (particularly cardiac glycogen) might be indicative of anoxic stress in neonate birds. If Northern Pintail ducklings have some energetic adaptation to withstand long overland movements, it could be relatively large glycogen stores rather than lipid reserves.

The effect of a 3 km walk on the growth of newly-hatched Northern Pintails was also examined. At 7 and 11 days of age, the weights of walked ducklings tended to be greater than that of controls (0.10 > P > 0.05), but there was no difference in the lengths of their tarsometatarsi or culmens (Fig. II-3). Because 2-2.5 week old male Mallard

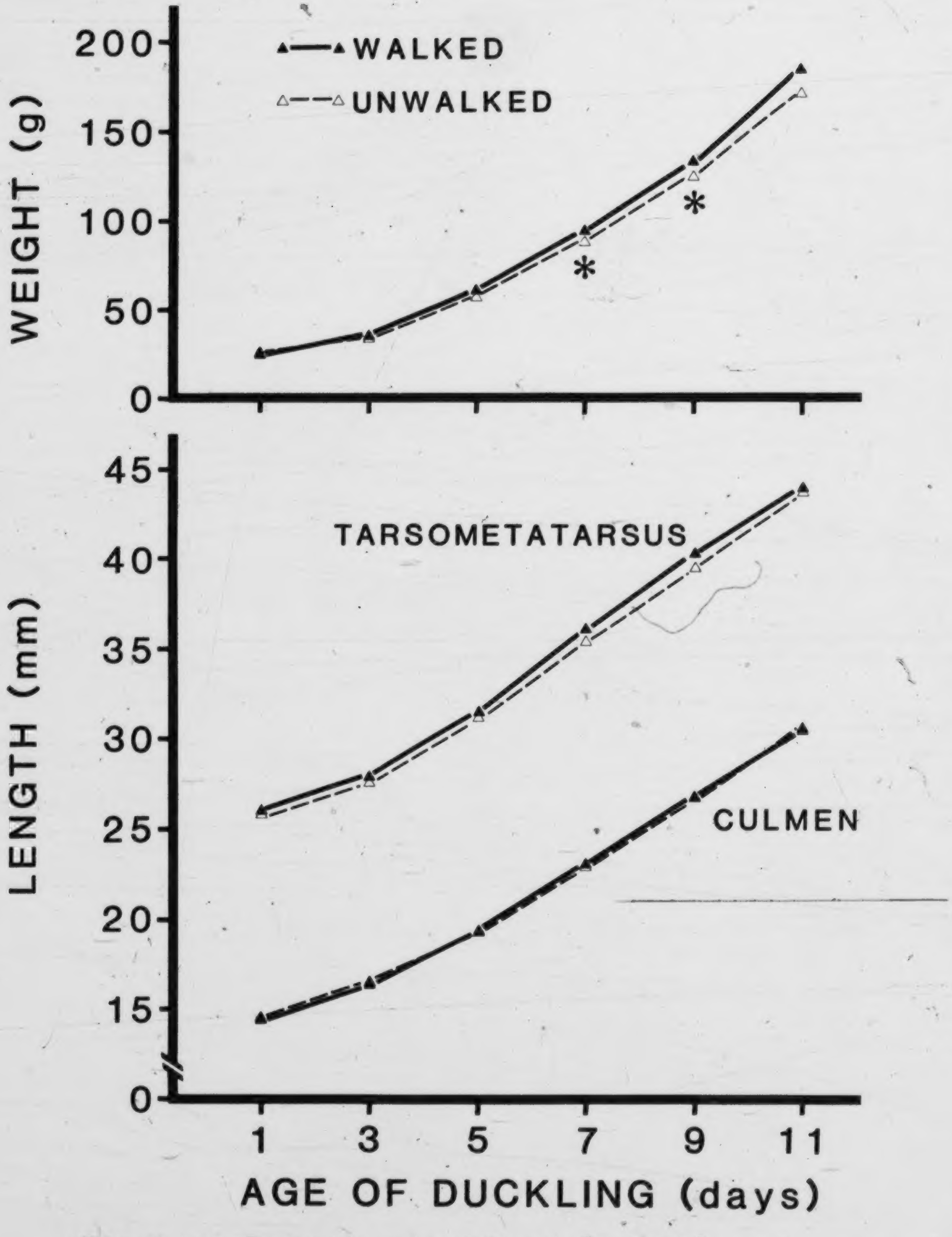

Fig.II-3. Growth of walked (n=21) and unwalked (n=19) Northern Pintail ducklings. * 0.10>P>0.05, two-way anova with random brood effect.

ducklings are larger than females (Rhymer 1982), I examined the sex ratio in both groups in case the walked group happened to have relatively more males. The sex ratio (males/females) was 0.5 for the walked group and 1.1 for the unwalked group such that any effect of sex would have acted in the opposite direction than found. The tendency for greater increase in weight in the walked ducklings could reflect increased feeding in response to greater metabolic demands after the walk. Thus, a 3 km nest-to-water movement by Northern Pintail ducklings appears to have no serious detrimental effect on their physiological condition.

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III. NESTING OF NORTHERN PINTAILS IN ALBERTA: LAYING DATE, CLUTCH SIZE, AND RENESTING

INTRODUCTION

The timing of egg-laying in birds is believed to be adaptive because it generally coincides with a seasonal abundance of food resources. Lack (1966) believed that the ultimate (sensu Baker 1938) factor governing the time of breeding was the availability of food for the young, although food resources for the production of eggs appear to be the primary factor influencing the timing of laying in some species (Perrins 1970). At the proximate level, photoperiod is known to influence the onset of the breeding season in many temperate zone birds although a number of environmental factors such as temperature, rain, vegetation changes, and protein availability can modify its effect, particularly in females (Farner and Follett 1979). The laying date of ducks appears to be affected by ambient temperature (Langford and Driver 1979, Cowardin et al. 1985), age of the hen (Krapu and Doty 1979, Baillie and Milne 1982, Afton 1984, Dow and Fredga 1984), and individual variation (Koskimies 1957, Spurr and Milne 1976, Batt and Prince 1979, Dow and Fredga 1984).

What ultimately determines clutch size in precocial birds is speculative, with the possible exception of some arctic-nesting geese (Winkler and Walters 1983). Lack (1967, 1968) suggested that the ultimate limitation on clutch size in ducks was food availability to laying hens modified by size of the egg. The clutch size of ducks appears to be affected by laying date (Koskimies 1957, Batt and Prince 1979), age of the hen (see Afton 1984 for review), individual variation (Koskimies 1957, Batt 1979), and possibly diet (Bengston 1971, Krapu 1981).

Renesting is the laying of a replacement clutch of eggs following an unsuccessful reproductive attempt by a single-brooded bird. In ducks, renesting may occur after loss of a clutch, and occasionally, after loss of a brood (eg. Sowls 1955, Strohmeyer 1967, Doty 1975). Food supply appears to regulate the extent of renesting in some bird species and the occurrence of second broods in a number of multi-brooded species (Soikkeli 1967, Cody 1971, Hilden 1975, Drent and Daan 1980). In ducks, food quality and availability on the breeding grounds are thought to regulate a hens ability to renest because her body reserves, which may be important for egg production, would have been depleted during the previous nesting attempt (Krapu 1974, 1979, 1981, Swanson and Meyer 1977). Protein is believed to be an important limiting nutrient in the diet of laying ducks of a number of species because: 1) almost half of the dry weight of duck eggs is protein, 2) labile protein reserves of the female are small , 3) females feed heavily on protein-rich invertebrates during laying, and 4) laying females consume relatively more invertebrates than do male (Krapu 1974, 1981, Krapu and Swanson 1975, Drobney and

Fredrickson 1979, Drobney 1980, 1982, Robbins 1981).

This paper examines laying date, clutch size and renesting in a wild population of Northern Pintails (*Anas acuta*) in southeastern Alberta. The effect of age of the hen (yearling vs. adult) on these reproductive traits is analyzed and the responses of birds to controlled, captive conditions is tested. The correlation between clutch size and laying date is examined and various hypotheses that have been suggested to explain this phenomenon are tested. The effect of two diets with differing protein content on renesting is also examined.

STUDY AREA AND METHODS

The study of the wild population was conducted in an area of grazed mixed grass prairie about 35 km south-east of Brooks, Alberta between 1981 and 1984. The study area included four impoundments which are managed for waterfowl production by Ducks Unlimited Canada. These are described by Giroux (1981; impoundments D, E, F and G). At high water levels, the areas of these impoundments were, respectively, about 0.7, 0.2, 2.0 and 0.75 km². Each basin contained artificial islands. The water in each impoundment was less than 1 m deep except for 1-2 m deep moats around the islands. During all years of the study, the main impoundment, F, retained more than 0.5 m of water over the summer, although in 1984, its area was reduced by about 50% by June. From 1981-1983, the water level in D, E, and G declined over the summer, so that by August there often existed little water outside of the moats. Impoundment G was dry during 1984 while D and E were greatly reduced in area and had less than 0.25 m of water.

Data on the reproductive traits studied was obtained from Northern Pintail nests found on both the islands and the mainland. Searches for nests on the artificial islands were conducted by walking across them systematically at least once every 3 weeks. On the mainland, nests were located by dragging a 50-80 m steel rope between two vehicles along parallel transects. The principal study plot on the mainland was adjacent to impoundment F, the largest and most permanent waterbody. Although this study plot varied in size among years, the annual nesting chronology of Northern Pintails was established only from data obtained from a mainland area that was systematically searched throughout the nesting season. The artificial islands were deemed unsuitable for constructing nesting chronologies of Northern Pintails because the rank vegetative growth which developed each summer could have altered the seasonal suitability of the islands for nesting Northern Pintails. In contrast, the physiognomic structure of the mainland prairie vegetation changed little throughout the season.

Duck nests were attributed to a species based on identification of the flushing hen, and occasionally, when this was not possible, by characteristics of the eggs and feathers in the nest. To obtain data on individuals, Northern Pintail hens were trapped on their nests using drop traps (Sowls 1949), modified Weller traps (Weller 1957), or bow-net traps (Sayler 1962). Hens were identified as either yearlings or adults based on wing-feather characteristics (Duncan 1985). All hens were weighed and banded to identify renesting individuals. In 1982, some hens were outfitted with solar-powered radio transmitters (Telemetry Systems, Mequon, Wisconsin) to examine renesting. The transmitters were attached to the birds using a harness design similar to that described by Dwyer (1972). The transmitter and harness weighed about 20 g. Some hens were also marked with nasal saddles in 1982.

The stage of incubation of the eggs was estimated by candling the eggs and using Weller's (1956) guide to embryo development. Laying date was calculated by back-dating from the stage of incubation and the number of eggs in the clutch. Clutch sizes of nests which had been parasitized or exhibited signs of partial clutch depredation were not used in the analyses of clutch size. The distance between first nests and those containing replacement clutches was estimated by vehicle odometer. Air temperatures were obtained from the monthly records of the Atmospheric Environmental Service of Environment Canada recorded at the Alberta Horticultural Research Station at Brooks.

During 1982, renesting was investigated in the wild using hens that were radio-tagged when captured. Some of these hens had their clutches removed at the time of capture, whereas others had their nest left intact but subsequently deserted as a result of capturing and handling. Locations of radio-tagged hens were checked every 3-7 days. It was assumed that all radio transmitters remained functional throughout the study and that inability to obtain a radio signal meant that the bird had left the study area.

In 1983, renesting was examined by banding and releasing all hens that could be captured and removing their clutches. The area over which the nest search and capture program was conducted was expanded late in the nesting season. In conjunction with this capture/recapture program, predator control was conducted on the study area to keep the natural clutch destruction rate to a minimum. Predator control efforts were aimed at Striped Skunks (*Mephites mephites*), California Gulls (*Larus californicus*) and Ring-billed Gulls (*L. delawarensis*).

To examine nesting under controlled conditions, Northern Pintails were hatched from eggs taken from the study area in 1983 and reared in captivity at the Brooks Wildlife Center of the Alberta Department of Energy and Natural Resources. The birds used for captive breeding were randomly selected from clutches taken throughout the nesting season. The birds were wing-clipped to prevent flight and maintained on an ad libitum commercial waterfowl maintenance diet until spring of 1984. The ducks were exposed to natural daylength but had access to relatively warm indoor facilities during the winter. Forty-one pairs of birds were placed into individual 4.6 x 9.2 m pens between March 26-April 2, 1984 where they were essentially visually isolated. Most of these birds had paired naturally, as identified by repulsion behavior of a female towards other males. Two hens that were very disturbed by human presence were replaced with other birds on April 24. The ground within the pens was sparsely vegetated in the early spring and secluded nest-sites were provided. Each pen contained a 46 x 33 x 12 cm water basin in which the water was changed daily. Half of the pens also had 2.2 x 2.3 m cement ponds which sloped to maximum depth of 0.2 m. The water in these ponds was changed infrequently, allowing stagnation and dense algal growth. Penned pairs were initially maintained on a 29% protein commercial waterfowl diet provided ad libitum (Shur-Gain Div., Canada Packers Inc.). Crushed oystershell was also provided ad libitum throughout the study. All clutches produced were removed on the third day of incubation to induce renesting. When the first clutches were taken, the diet of every second pair was changed to a 14% protein commercial feed (Shur-Gain Div., Canada Packers Inc.) to examine the effect of diet on renesting. All birds were removed on June 28-29 after nesting activity had ceased. Birds were weighed immediately before being confined to breeding pens. For the analyses of clutch size of captive birds, I used only incubated clutches which were laid within a single nest bowl without any eggs being "dropped" during laying, or within 7 days of clutch initiation. This eliminated potential error when abnormally large "clutches" resulting from continuous laying are included. Continuous laying occurs when birds disrupted during the laying sequence, desert their nests, but continue to deposit eggs in a new nest without a break in the laying cycle, that is, the time interval between successive eggs does not change (Sowls 1955).

Statistical analyses were performed using the SPSSX package. The significance level was set at alpha = 0.05; non-significant values are indicated by NS. When means are presented, they are followed by standard errors. Regression analyses were conducted using polynomial, natural logarithm, and inverse transformations in addition to the straight-line regressions. A non-linear regression was used only when it significantly increased the goodness-of-fit (Kleinbaum and Kupper 1978). The non-linear model which produced the greatest correlation coefficient was used although there was generally little difference in the explanatory power of the 3 models.

RESULTS

Laying Date

In the wild, Northern Pintails initiated nests over a 9 week span in 1982 and 1983, but only over 5 weeks in 1984 (Fig. III-1). Each year, Northern Pintails began laying in April, reaching a peak in clutch initiations during the

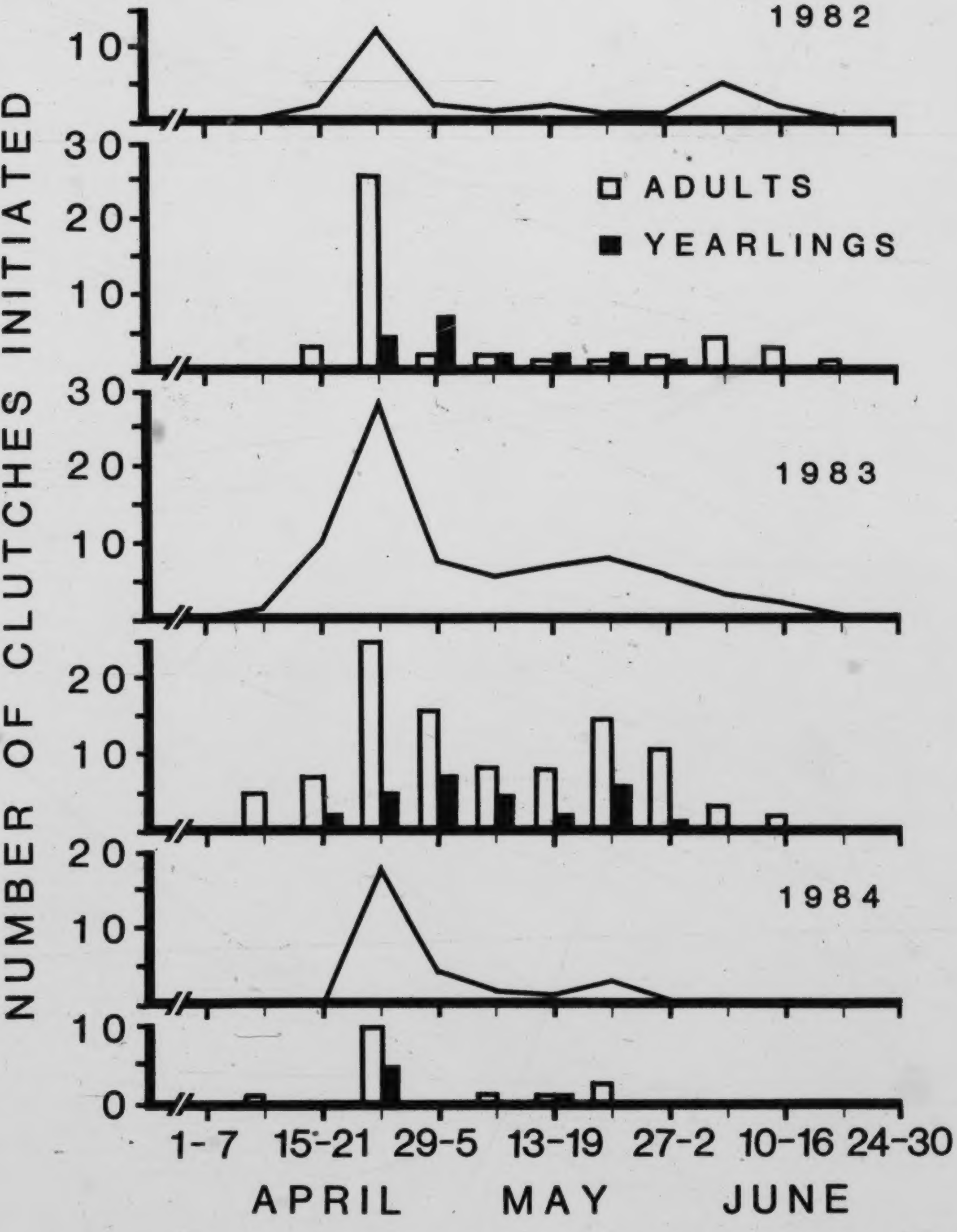

Fig.III-1. Chronology of clutch initiation on study plots and frequency distribution of adult and yearling Northern Pintails initiating clutches on study area in southern Alberta, 1982-1984.

fourth week of April. Although too few nests were found on the study plot in 1981 to construct a meaningful chronology of clutch initiations, nesting began earlier in that year; considering only those nests started in April, the mean laying date in 1981 was 18 April, as opposed to the 25, 23 and 25 April in 1982-1984 respectively (ANOVA, $F = 22.2$, $P < 0.0001$). No relationship was found between mean April daily temperature, mean minimum April daily temperature, or heat sum (cumulative daily means > 0°C) in the third and fourth week of April, and mean clutch initiation date in April. The mean temperature in April of 1981 was similar to that in 1984 (6.5 vs. 6.3°C), and despite the variable mean temperatures in 1982-1984 (1.9, 4.8, and 6.3°C respectively), nest initiation during April was similar in each of those 3 years. After the initial peak in clutch initiations, relatively few new clutches were started over the last 4 to 7 weeks (Fig. III-1). A very minor secondary peak in clutch initiations was recorded late in the nesting season.

Adults were the earliest birds to nest each year and were primarily responsible for the April nesting peak (Fig. III-1). Yearlings initiated a relatively greater proportion of the clutches in May than in April. Because the nesting chronologies during 1982-1984 were similar, laying dates in these 3 years were combined for adults and yearlings to analyze age-related differences in laying dates. Considering only clutches initiated prior to May 16, so as to exclude renesting attempts (see below), the mean laying date of adults was 5 days earlier than yearlings during 1982-1984 (April 27, n = 108 vs. May 2, n = 37; $t = 3.13$, $P < 0.005$). Clutch initiations by adults increased relative to those of yearlings in late May, and by June essentially only adults were starting clutches.

Yearling Northern Pintails initiated clutches over a 7-week span in captivity. The peak in clutch initiations among captive Northern Pintails was earlier than that for wild birds in 1984 (Fig. III-2). Considering only those clutches started in April, the mean laying date of the captive birds was 4 days prior to that of all wild birds (April 21, n = 32 vs. April 25, n = 24; $t = 3.92$, $P < 0.001$). The advanced nesting in captivity occurred despite the fact that the captives were yearlings and most wild birds were adults.

The body weight of wild birds when captured during incubation was not correlated with laying date, when all nests were considered ($r^2 = 0.02$, n = 112, NS), nor when the analysis was restricted to laying dates prior to May 1 ($r^2 = 0.03$, n = 45, NS). Likewise, the body weight of captive birds prior to nesting was not related to laying considering all nests ($r^2 = 0.00$, n = 39, NS), or when restricted to first nests ($r^2 = 0.05$, n = 30, NS).

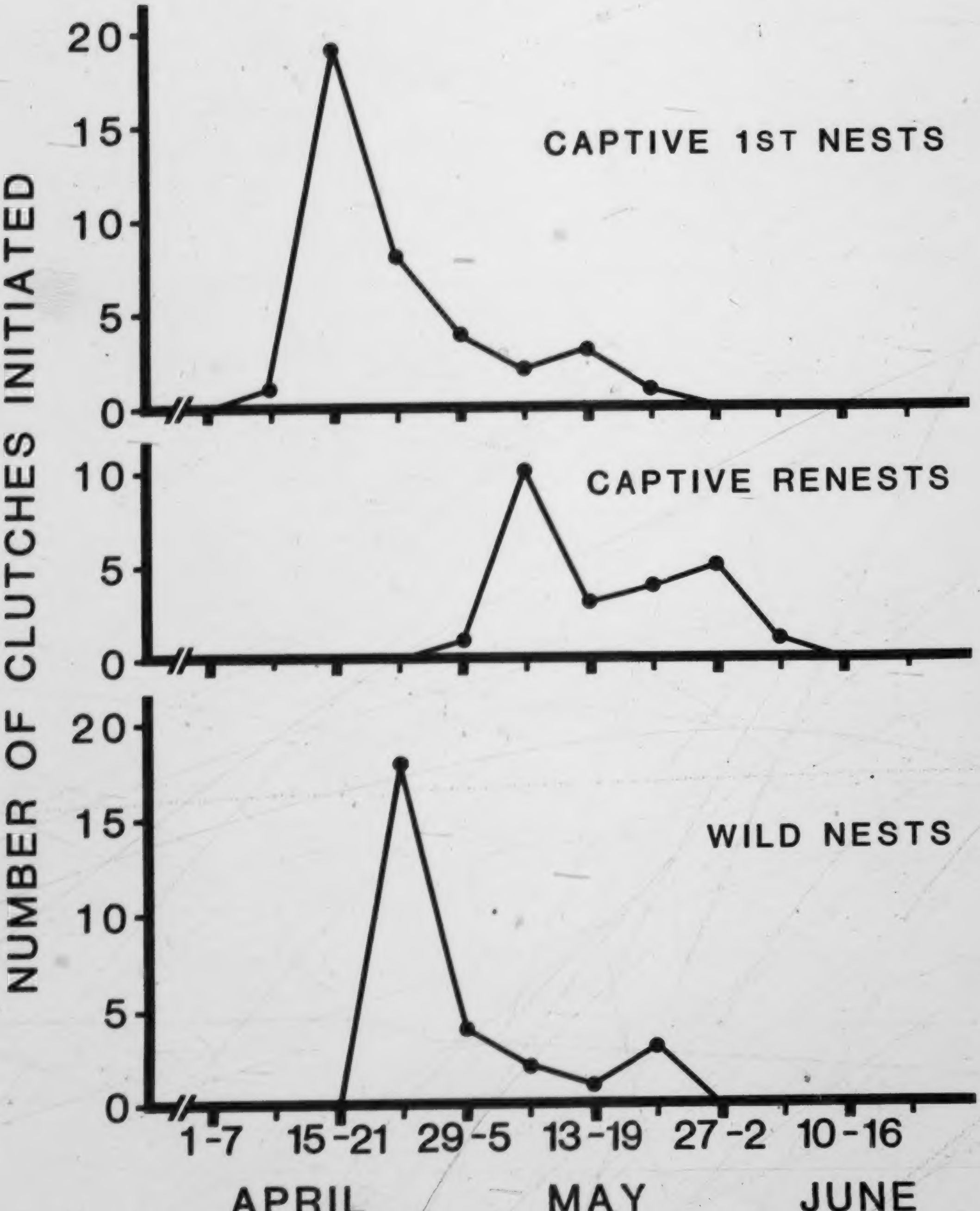

Fig.III-2. Chronology of clutch initiation for captive and wild Northern Pintails in southern Alberta during 1984.

Clutch Size

The mean clutch size of Northern Pintails in the wild over the 4 years of the study was 6.9 ± 0.1 (Fig. III-3). Clutch size decreased with later laying date until the end of May in each year (Fig. III-4). In the 2 years when clutches were initiated well into June (1982 and 1983), the relationship between clutch size and laying date was best described by a polynomial regression showing that the mean clutch size increased slightly in June. An analysis of covariance revealed no difference between the 4 years considering all the data ($F = 1.15$, NS), and when considering only nests initiated prior to May 11 such that each annual relationship was linear ($F = 1.31$, NS). Combining the data from all 4 years, a polynomial relationship best described the relationship of clutch size to laying date (Fig. III-5). The captive flock of yearlings also exhibited a seasonal decline in clutch size (Fig. III-6). This relationship persisted when the analysis excluded renest clutches ($r^2 = 0.18$, $n = 25$, $P < 0.05$). Analysis of covariance to control for the effect of laying date revealed that the captive birds laid larger clutches than did all wild birds (adjusted $\bar{x} = 8.1$, $n = 41$ vs. 6.9, $n = 290$, $F = 37.6$, $P < 0.001$.). Analysis of covariance adjusting for laying date also revealed that the clutch size of renesting captive birds did not differ from that of captives nesting for their first time (1st nests, adjusted $\bar{x} = 8.2$, $n = 25$; 2nd nests, adjusted $\bar{x} = 8.3$, $n = 16$; F =

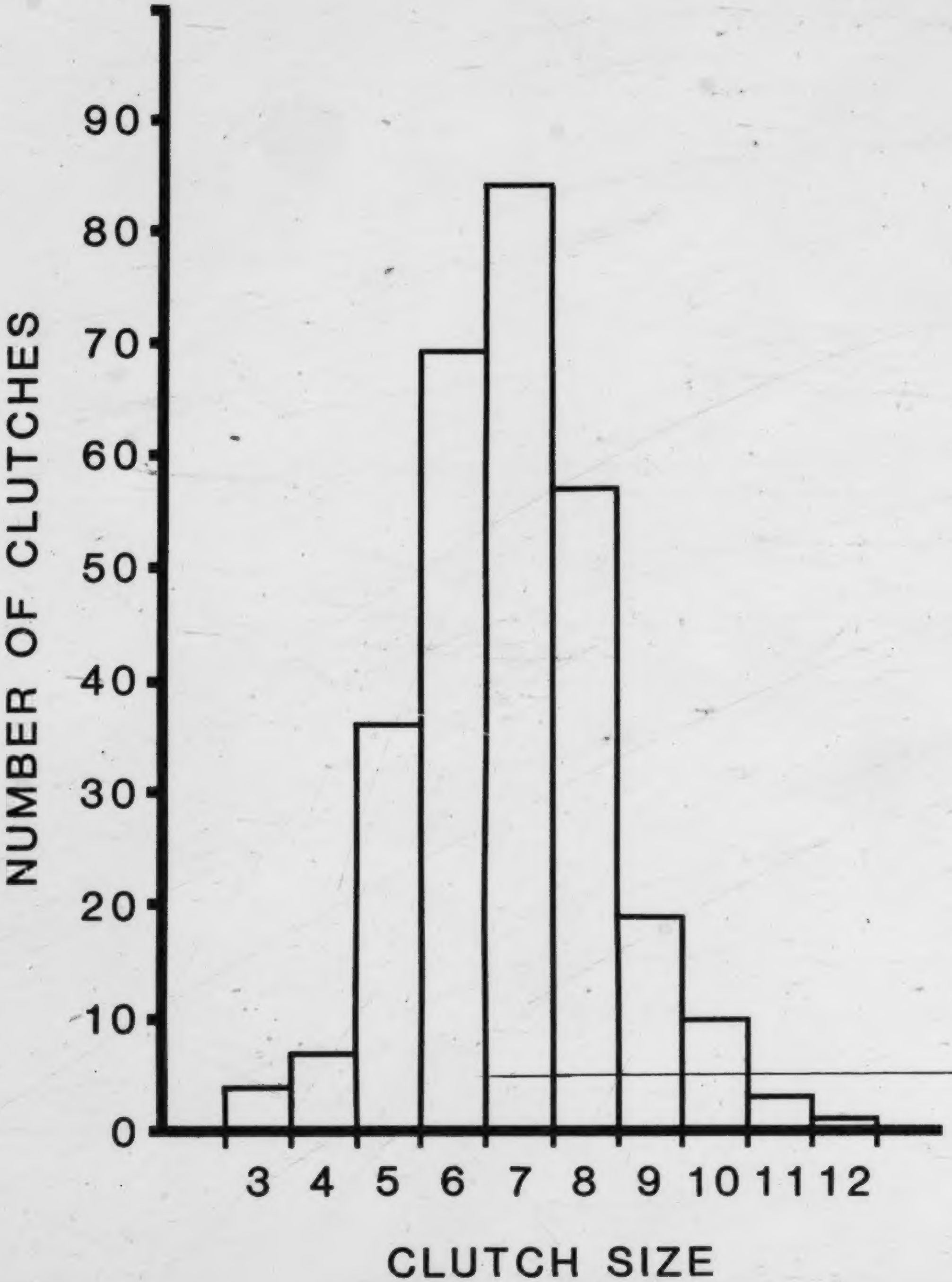

Fig.III-3. Frequency distribution of clutch size of Northern Pintails in southern Alberta.

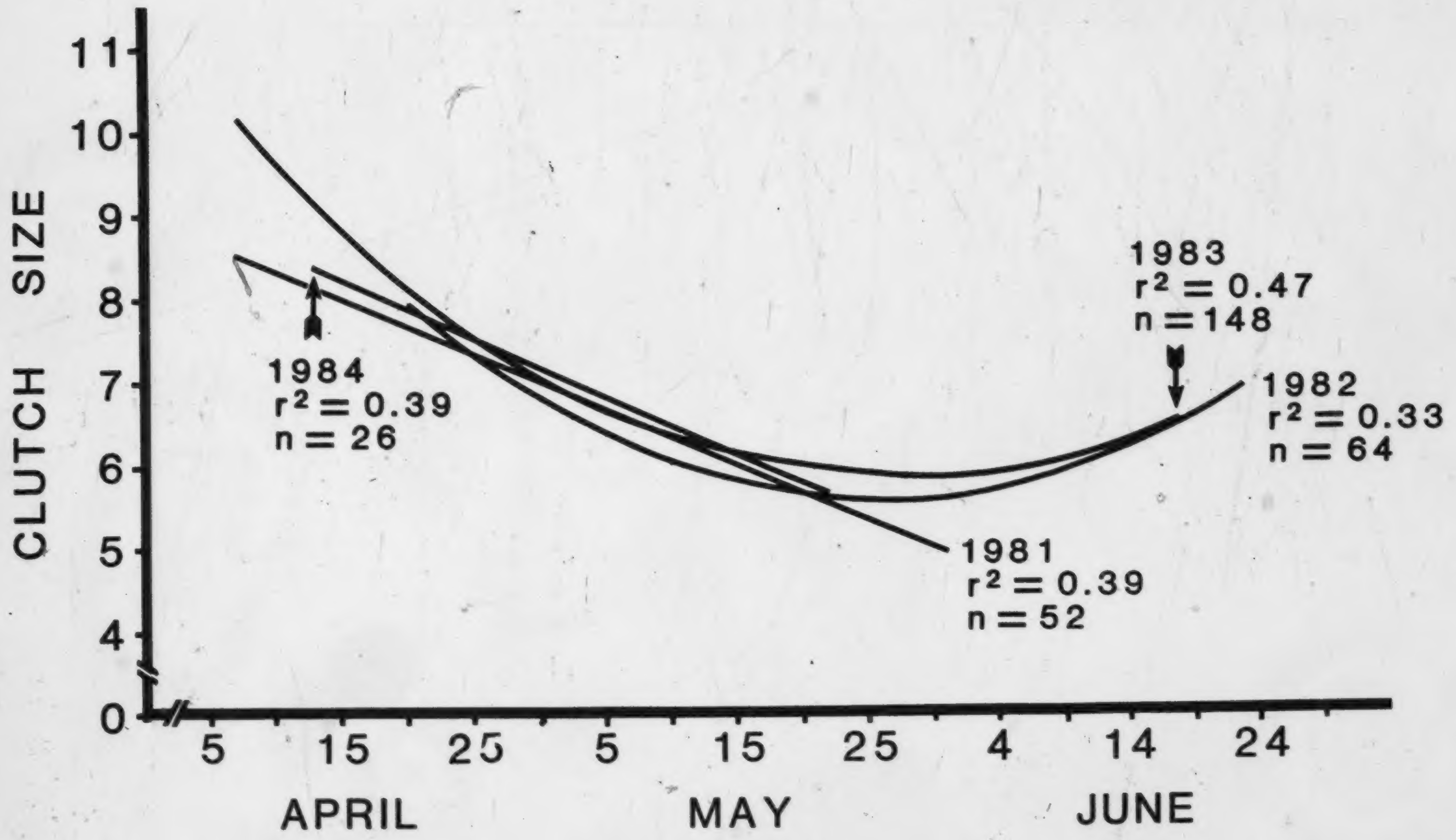

Fig.III-4. Relationship between clutch size and laying date for Northern Pintails nesting in southern Alberta, 1981-1984. For each regression, $P < 0.001$.

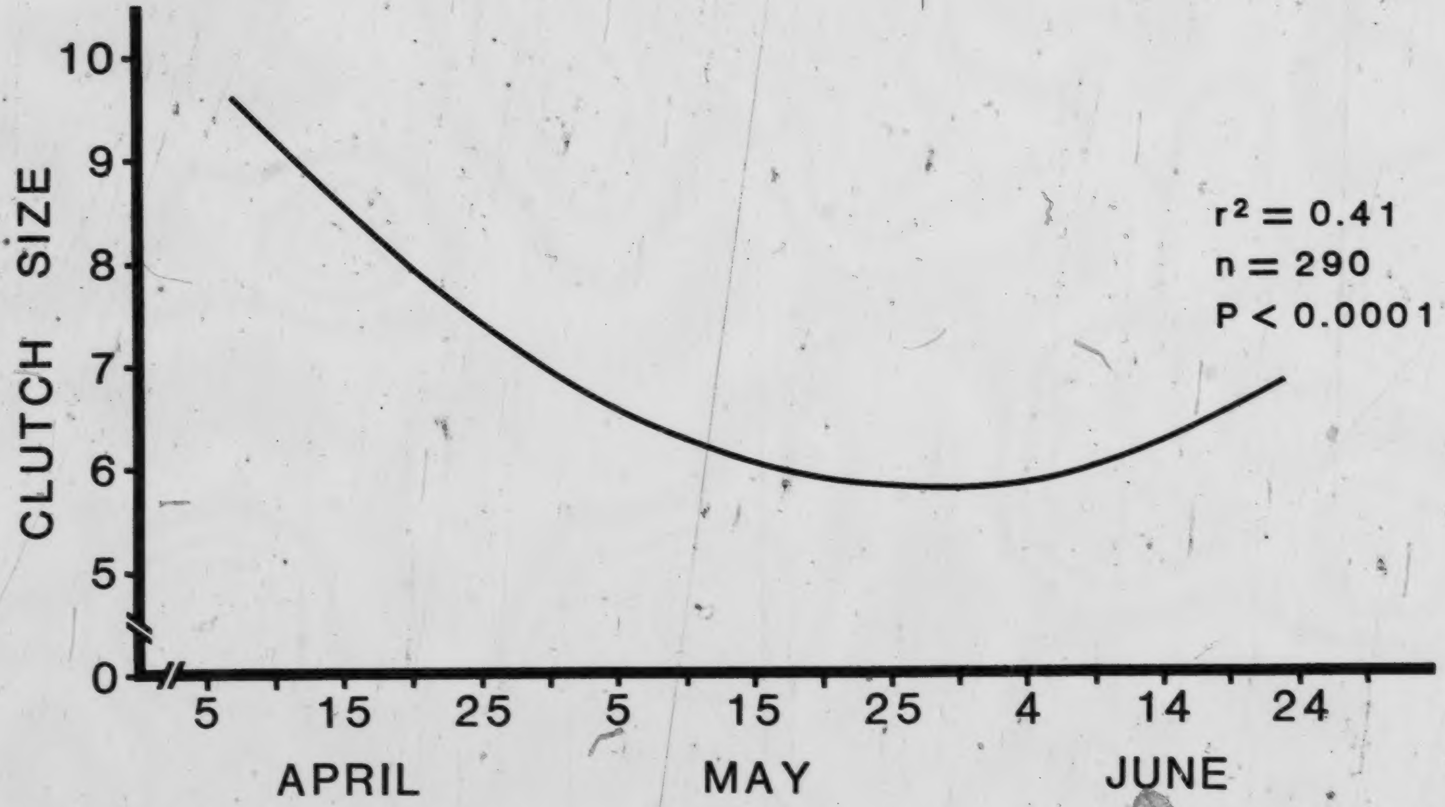

Fig.III-5.Relationship between clutch size and laying date for Northern Pintails nesting in southern Alberta, 1981-1984 combined; $y = 10.718 - 0.171x + 0.0015x^2$.

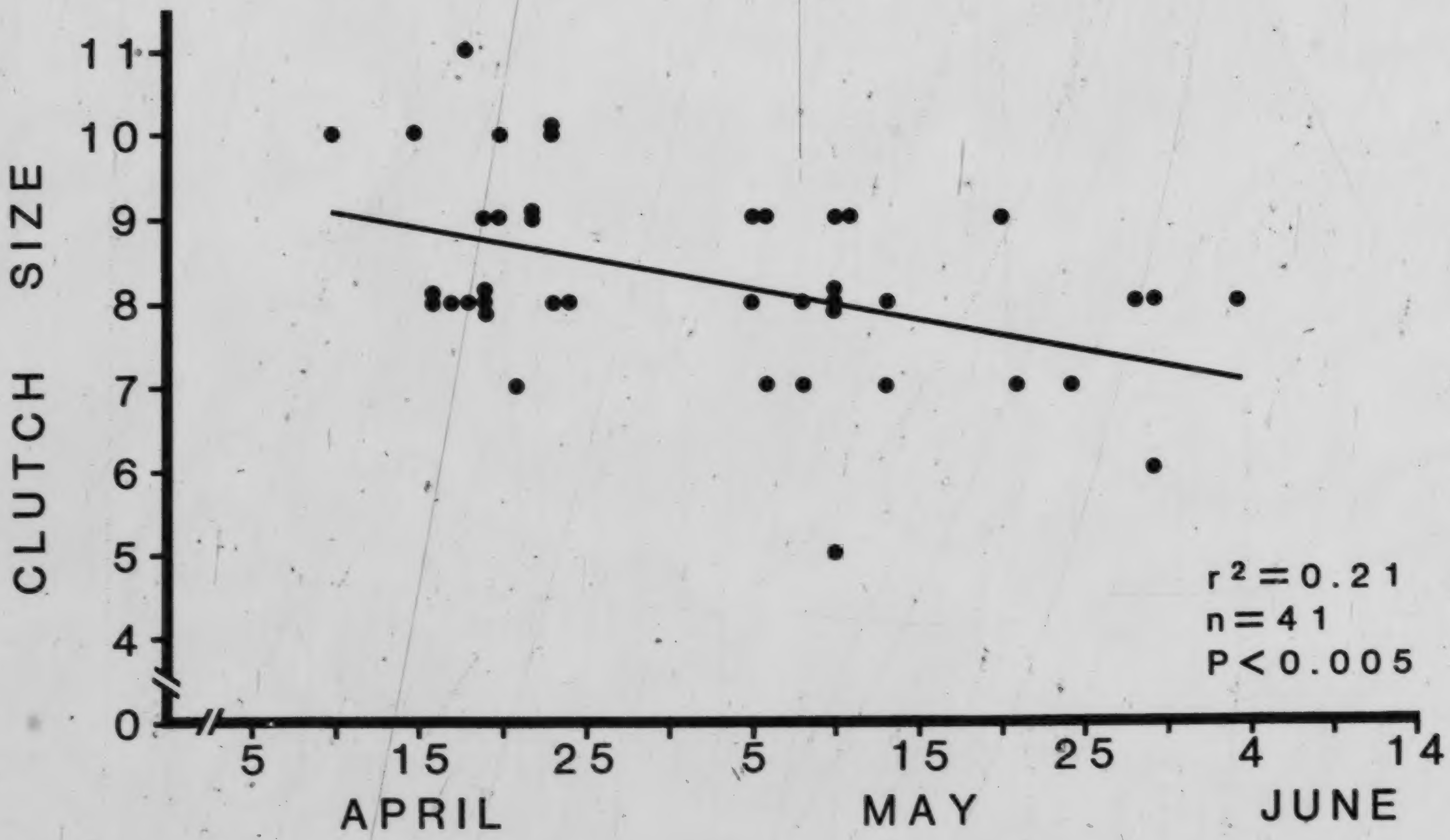

Fig.III-6. Relationship between clutch size and laying date for captive yearling Northern Pintails; $y=9.45-0.037x$.

0.01, NS).

When clutch size and laying date were examined for wild yearlings and adults separately, an analysis of covariance again showed that there was no difference among years in clutch size (yearlings, $F = 0.22$, NS; adults, $F = 0.10$, NS). The data from 1982-1984 was subsequently combined for the analyses of each age class. Both adults and yearlings exhibited a seasonal decline in clutch size, although the shape of the relationship differed between the age classes (Fig. III-7). The clutch size of yearlings was smaller than that of adults in an analysis of covariance that accounted for laying date when all nests were considered ($F = 9.3$, $P < 0.005$), and when only adults nesting concurrently with yearlings were considered such that the adult relationship was also straight-line ($F = 6.1$, $P < 0.05$).

The body weight of wild birds during incubation and of captive birds prior to nesting was not correlated with the clutch size when all nests were considered ($r^2 = 0.00$, $n = 106$; $r^2 = 0.01$, $n = 42$; respectively, NS), or when the analyses were restricted to nests initiated prior to May 1 in the wild and to first nests for the captive flock ($r^2 = 0.01$, $n = 41$; $r^2 = 0.00$, $n = 25$; respectively, NS).

Renesting

In 1982, renesting was examined using 17 wild radio-tagged hens which had lost their first clutch. All hens were captured before May 23; 14 before May 13 (Fig.

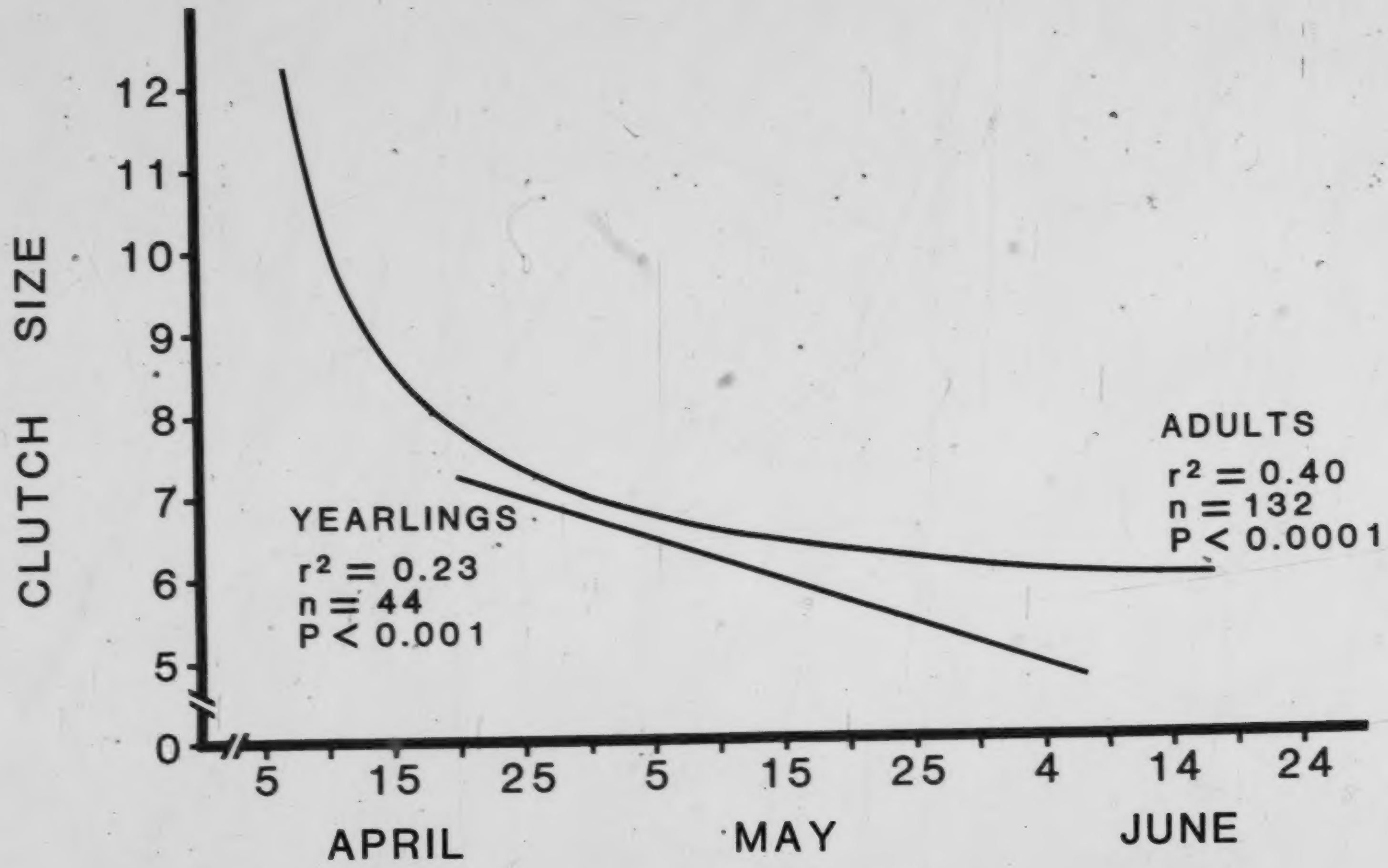

Fig.III-7. Relationship between clutch size and laying date for adult ($y = 5.36 + 48.44 \frac{1}{x}$) and yearling ($y = 8.25 - 0.05x$) Northern Pintails nesting in southern Alberta, 1982-1984 combined.

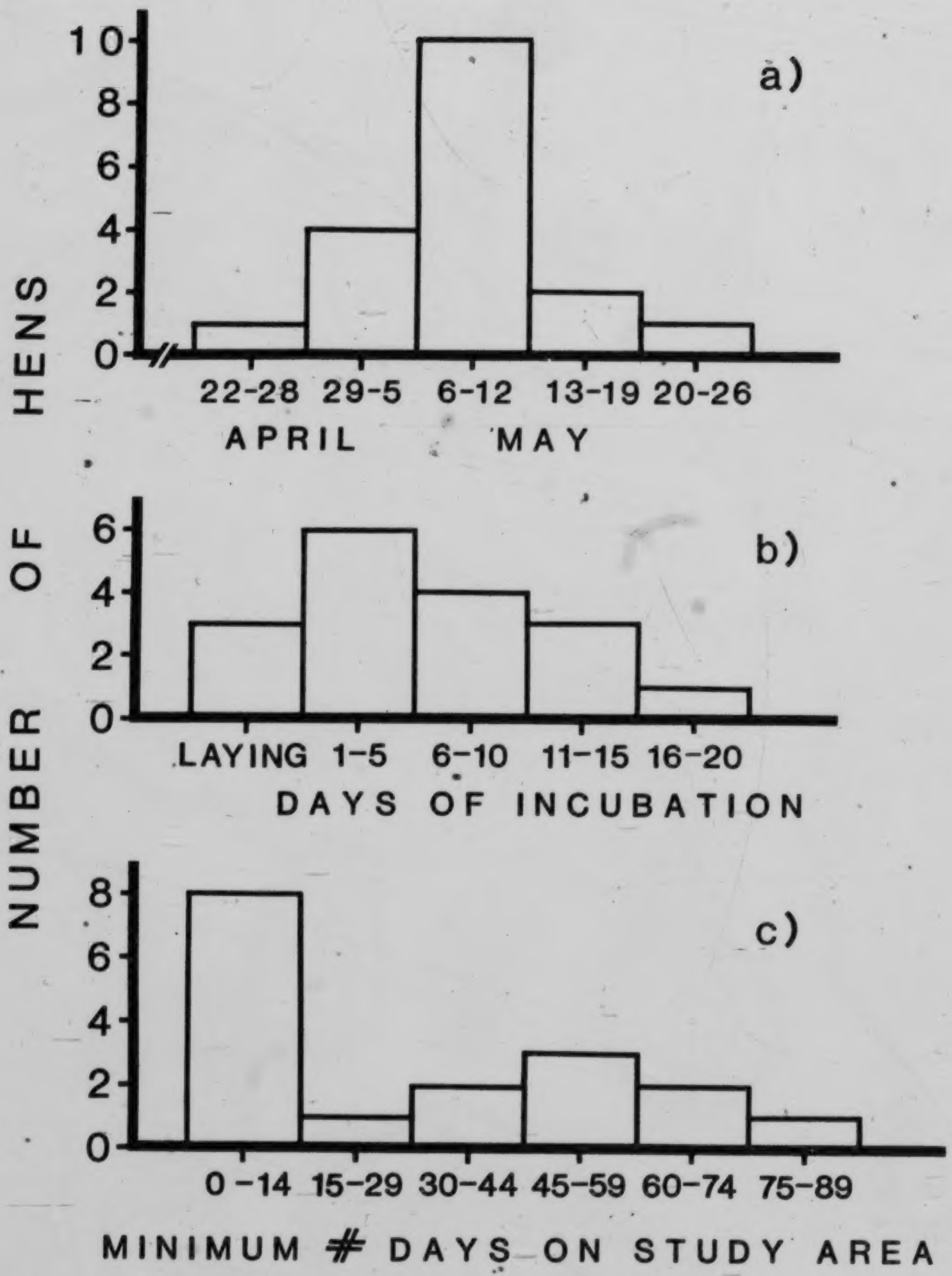

Fig.III-8. Status of wild Northern Pintail hens that were radio-tagged in 1982: a) date of capture, b) stage of nesting when captured, and c) time that hen remained on study area after capture.

III-8a). Because all hens had initiated their clutches before May 6 and thus were part of the early peak in clutch initiations, it is unlikely that any were renesting when captured. Most hens were caught early in incubation; 13 were captured prior to 11 days of incubation (Fig. III-8b). Because clutches were initiated as late as the third week of June in 1982, there presumably existed ample time for the hens to renest. None of the hens was found renesting. Eight of the hens remained on the study area for a minimum of 30 days after capture whereas eight others left within 2 weeks of capture (Fig. III-8c). Most of the hens that were captured around the three smaller impoundments (D, E, and G), and remained on the study area for at least 1-2 weeks, eventually moved 2-6 km to impoundment F, the largest and most permanent waterbody on the study area. This movement data and that of a few other hens which moved temporarily to other waterbodies 25 km away supported the assumption that absence of a radio signal meant that a bird had moved off the study area.

Although radio-tagged ducks are known to renest (eg. Krapu 1979, Cowardin et al. 1985), markers such as radios may adversely affect renesting behavior of birds (Amlaner et al. 1979, Parker 1981). Consequently, renesting was investigated without the use of radio telemetry in 1983. In total, 127 hens were captured, banded and released, and their eggs taken to induce renesting. At least 50% of these birds probably had not renested previously that year, because their clutches had been initiated in the first nesting peak (Figs. III-1 and III-9a). Approximately 30% of the hens were captured before the middle of May (Fig. III-9b). Only five hens were found renesting. These hens were first captured between May 3 and 15. Four of the five hens were captured before day 10 of incubation and had renesting intervals [the number of days between loss of a clutch or brood and initiation of another clutch (Sowls 1955)] ranging from 16-28 days (Table III-1). The fifth hen was captured on day 14 of incubation and had only a 9-day renesting interval. The clutch size of three hens decreased between the first and second nesting attempt whereas that of the other two hens remained the same. The median distance between first nests and the site of renesting was 300 m (Table III-1).

I believe that the low number of hens that I recorded renesting was a realistic representation of the frequency of renesting in this population. This belief assumes that hens renest within a few hundred meters of their first nest-site (eg. Sowls 1955, Strohmeyer 1967) and is based on the following rationale. The natural hatch success rate of all Northern Pintail clutches that I found in 1983 was 72% using the Mayfield method (Miller and Johnson 1978), and thus, the probability that clutches were destroyed by predators before I found them was relatively low. The success rate for capturing hens once a nest had been found was 69%. I do not believe that trapping success was biased towards naive birds

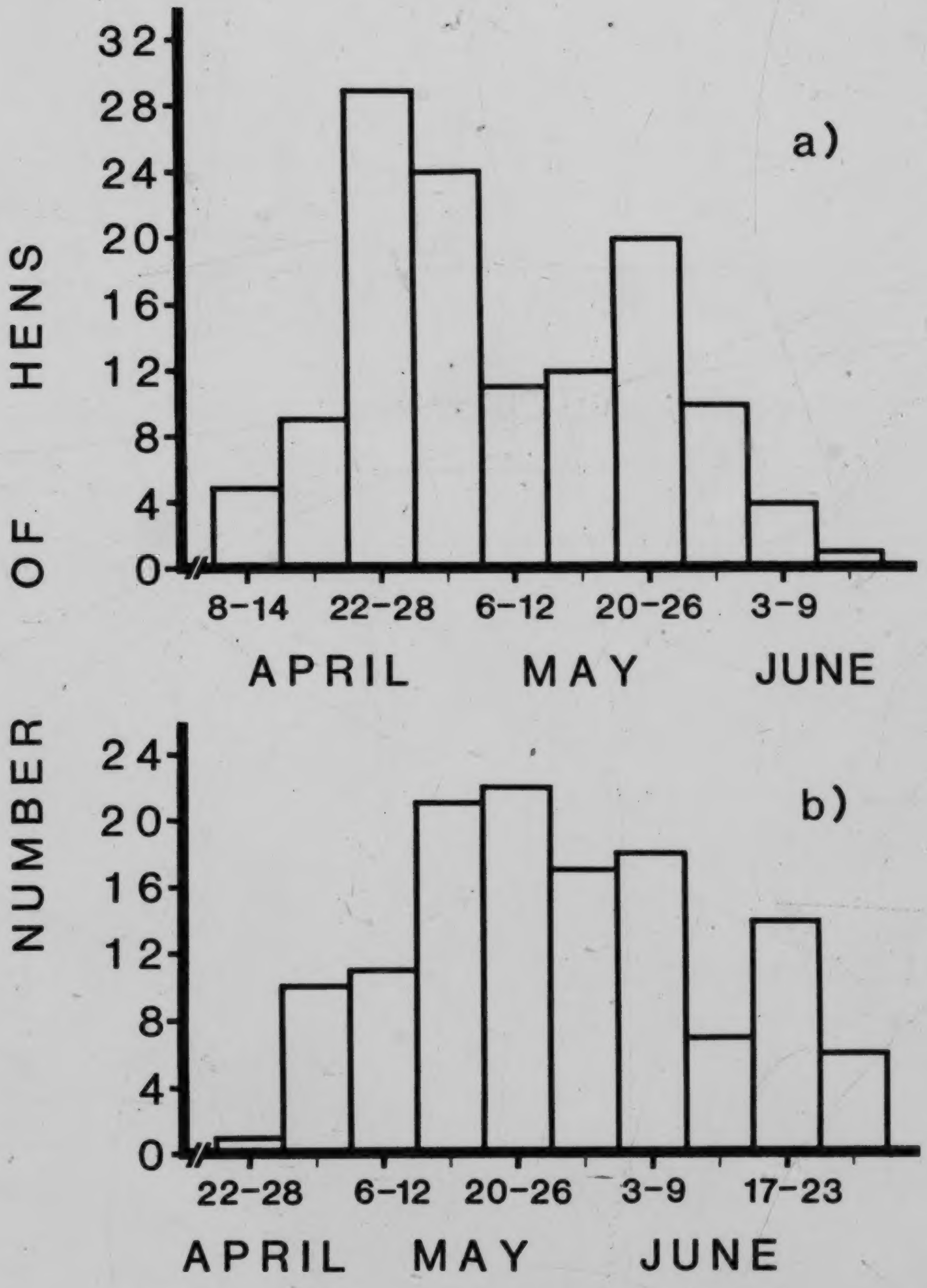

Fig.III-9. Status of Northern Pintail hens captured in 1983: a) laying date, and b) date of capture.

Table III-1. Renesting characteristics of five wild Northern Pintails in southern Alberta during 1983.

Laying date of 1st nest	Incubation at capture (days)	Laying date of 2nd nest	Renest interval[a] (days)	Clutch size		Distance between nests (m)
				1st nest	2nd nest	
April 21	7	May 31	26	8	5	300
April 23	14	May 24	9	9	5	750
April 24	9	June 6	28	7	5	500
April 25	3	May 23	20	6	6	100
May 1	6	May 28	16	6	6	300

[a] Time between loss of 1st clutch and initiation of laying of replacement clutch.

because unsuccessful trapping attempts were seldom caused by birds not entering the trap; the last 9 hens to be trapped were collected as a precaution against that likelihood (only 1 was a renesting bird). In addition, the nest initiation chronology in 1983 was very similar to that of 1982 despite the induced 0% nest success rate in 1983 (Fig. III-1). The increased proportion of adults initiating nests during May in 1983 compared to 1982 (Fig. III-1) may have been the result of increased renesting effort.

In the captive flock, protein content of the diet (14% vs. 29%) had no effect on the proportion of hens renesting, clutch size, renesting interval or rate of laying (Table III-2). Overall, 50% of the hens that produced a first clutch renested. Birds that renested initiated their first clutches earlier than those that did not renest ($\bar{x}$ = April 21, n = 19 vs. May 1, n = 19; t = 2.96, $P < 0.01$). Despite this difference, 36% of the 28 hens laying before May 1 did not renest. The average renest interval for all birds was 9.6 ± 0.6 days (n = 25). The renesting interval was not related to the date on which the first clutch was taken (r = 0.05, n = 24, NS).

DISCUSSION

Laying Date

Contrary to the results of this study, ducks have been reported to nest earlier when spring temperatures are higher

Table III-2. Renesting characteristics of female Northern Pintails on two diets with different protein content.

Protein level of diet	Number of hens on diet	Number of hens renesting once (%)	Median renest interval[a] (*n*)	Median clutch size (*n*)	Number of hens renesting twice (%)	Median renest interval[a] (*n*)	Median clutch size (*n*)	Rate of laying[b]
14%	18	10 (55.6)	9.5 (10)	7.5 (6)	3 (16.7)	12.0 (3)	7.0 (2)	0.96
29%	20	9 (45.0)	9.0 (8)	8.0 (5)	4 (20.0)	7.5 (4)	8.0 (3)	0.96
Combined	38	19 (50.0)	9.0 (18)	8.0 (11)	7 (18.4)	10.0 (7)	8.0 (5)	0.96

[a] Days

[b] Eggs/day; calculated between first and last eggs within a laying sequence including dropped eggs.

(Sowls 1955, Langford and Driver 1979, Hammond and Johnson 1984, Cowardin et al. 1985). The earlier laying by captive Northern Pintails compared to those in the wild, despite similar temperatures, shows that some other environmental factor affects time of nesting. The advanced nesting in captivity may have been caused by the ad libitum, high quality food resources available to the captive birds acting either directly or through improved body condition. Food availability for laying female ducks has been suggested as an important factor affecting clutch initiation in ducks (Vaisanen 1974, Krapu 1974, 1981). Krapu and Doty (1979) speculated that earlier nesting by Mallards (*Anas platyrhynchos*) in warmer springs could be a result of the influence of temperature on food availability. The correlation between early nesting and warmer temperatures in other species of birds has often been attributed to the influence of temperature on food accessibility (Perrins 1965, Bryant 1975, Slagsvold 1975, Dhondt et al. 1984, Newton and Marquiss 1984). Food availability has been shown to be important in regulating the onset of laying in wild birds by the provision of supplemental food (see review in Davies and Lundberg 1985). The lack of a relationship between clutch initiation and temperature in wild Northern Pintails could have resulted from a lack of dependance between availability of food resources and temperature under the climatic conditions experienced during this study. Under more extreme conditions a relationship may become evident;

Smith (1968) stated that freezing temperatures in mid-April caused a delay in nesting activity of Northern Pintails in southern Alberta.

Despite the relatively low environmental heterogeneity found under captive conditions, captive Northern Pintails exhibited considerable variability in laying date with clutches being started over a 7-week span. In a number of species of waterfowl, individual females have fairly consistent relative laying dates (Koskimies 1957, Spurr and Milne 1976, Batt and Prince 1979, Dow and Fredga 1984), apparently from inherited factors (Batt and Prince 1978, Birkhead et al. 1983, Findlay and Cooke 1983). Individual variation in laying date has also been found in some other species of birds (Brooke 1978, Nol et al. 1984), and is believed to have a genetic basis (van Noordwijk et al. 1980, 1981). Numerous researchers have attributed individual differences in laying dates to the existence of inherent variation, possibly mediated through feeding ability (Perrins 1965, 1970, Lack 1968, Spurr and Milne 1976, Houston et al. 1983, Cooke et al. 1984). Genetic variation might account for some of the differences in laying date of captive Northern Pintails. The advanced laying of captive Northern Pintails compared to those in the wild would appear to illustrate that earlier laying in the wild was being prevented by some environmental factor as opposed to genetic limitation. In this study, as in numerous others, a proportion of the population nested earlier than the majority (ie. prior to the peak) despite selective pressures favoring early nesting (see below). It has been suggested that this situation exists because of a trade-off whereby early nesting is beneficial to the survival of young but detrimental to the survival of the parents, such that the earliest nesting individuals may be at a disadvantage (Drent and Daan 1980, Dow and Fredga 1984). Because earlier laying in Northern Pintails is limited by some proximate, environmental factor, a simpler explanation is that laying date is food-limited and the earliest nesters are simply the result of natural variation in some food-related parameter in the population or environment.

Yearling Northern Pintails nested later than did adults in the wild. Earlier laying by older birds has been reported in various species of waterfowl (Finney and Cooke 1978, Batt 1979, Krapu and Doty 1979, Baillie and Milne 1982, Afton 1984, Dow and Fredga 1984). Afton (1984) suggested that later breeding by younger Lesser Scaup (*Aythya affinis*) may be a component of a "strategy" to maximize lifetime fitness as has been proposed in other groups of birds (Birkhead and Nettleship 1982, Oring and Lank 1982, Bryant and Westerterp 1983, Pugesek 1983, 1984). The fact that captive yearling Northern Pintails laid earlier than even adults in the wild, shows that yearlings have the physiological capability to lay early but are prevented from doing so in the wild by some proximate, environmental factor. Thus, the later laying date of yearling Northern Pintails in the wild does not result from a fixed ultimate "strategy" although a genetically plastic response cannot be ruled out. Similarly, Batt and Prince (1978) found that in captivity, yearling Mallards laid as early as adults. Two major hypotheses have been proposed to explain later breeding by younger birds of various species in the wild: 1) younger birds are inexperienced at finding food (Lack 1968, Nur 1984), and, 2) younger birds are socially inferior and are excluded from breeding space and/or resources (Wynne-Edwards 1962, Hannon et al. 1982). Delayed nesting by first-time breeders might also result from a general lack of experience resulting in later arrival on the breeding ground (Soikkeli 1967, Massey and Atwood 1981, Oring and Lank 1982), less well-developed behavioral repertoires (Dane and Van der Kloot 1964, Korschgen and Fredrickson 1976, Bruggers and Jackson 1981, Furness 1984), and decreased efficiency in territorial defense (DeSteven 1980, Cooke et al. 1981, Birkhead et al. 1983). Sowls (1955) reported that adult female Northern Pintails homed to their breeding ground earlier than did hand-reared yearlings. Some studies of food supplementation of wild passerines have shown that the laying date of yearlings is advanced more than that of adults (Kallander 1974, Smith et al. 1980), and a number of studies have indicated that younger birds, particularly in Larids, may be less efficient foragers (see Nur 1984 for review). The evidence suggests that later laying by younger birds is related to food acquisition. The lack of territorial behavior in breeding Northern Pintails (Smith 1968, Derrickson 1978, Titman and Seymour 1981) would appear to preclude the social exclusion hypothesis as an explanation for delayed breeding by yearlings. Although the precise mechanism is unknown, the inexperience hypothesis appears to be a more credible explanation for delayed breeding by yearling Northern Pintails than the social exclusion hypothesis.

Laying date was not related to body weight in Northern Pintails. In a few species of birds, there is some evidence that smaller (Jones 1971 cited by Dunn 1976, Price 1984), or heavier (Loman 1984) individuals may breed earlier than average.

In summary, laying date in Northern Pintails is affected by hen age, environmental conditions and likely individual variation. Food availability and foraging efficiency may be involved in the age-related and environmental differences of laying date.

The adaptive significance of the early spring nesting of Northern Pintails relative to other ducks remains speculative. Because food habits of newly-hatched ducklings of various species are similar (Sugden 1973), the hypothesis that food availability for the young governs laying date of various species of ducks would have to pertain to the diet of older ducklings when their diets have diverged. The availability of food for laying females is the other, most likely ultimate factor that could govern timing of nesting.

The overall adaptive value of laying date in various species of ducks is evidenced by the reduced survival rate of ducklings that are hatched relatively late in a species' breeding season (Hilden 1964, Grice and Rogers 1965, Bengston 1972, Dow and Fredga 1984, Hill 1984). This reduction in survival rate of later hatched young is also apparent in many other species of birds (Perrins 1970, Drent and Daan 1980, Cooke et al. 1984).

Clutch Size

The clutch size of the Northern Pintail is lower than that of other North American dabbling ducks and many diving ducks. This relatively low fecundity may be related to the Northern Pintail's relatively high survival rate compared with many other species of ducks (Bellrose 1976). A negative relationship between fecundity and adult survival is a common life-history correlation in birds (Cody 1971, Ricklefs 1977).

The clutch size of wild Northern Pintails in this study is very similar to that reported by Keith (1961) from southern Alberta, but lower than that found at Delta, Manitoba (Table III-3). Although a statistical comparison between Sowls' (1955) data from Delta and my sample was not possible, I was able to compare my data with a smaller sample from the Delta area recorded by Jones (pers. comm.) between 1977-1984. Analysis of covariance adjusting for laying date showed that the clutch size of Northern Pintails

Table III-3. Comparison of clutch sizes of the Northern Pintail from different areas.

Source	Location	Clutch completed by May 15	Clutch completed after May 15	n
Sowls 1955	Delta, Manitoba	9.0	7.1	105
Jones pers. comm.	Delta, Manitoba	8.3	7.6	41
Keith 1961	Gem, Alberta	7.2	6.2	79
This study-wild	Brooks, Alberta	7.4	6.0	290
This study-captivity	Brooks, Alberta	8.5	7.9	41

at Delta, Manitoba is larger than that of wild birds at Brooks, Alberta (adjusted $\overline{x} = 8.5$, $n = 41$, vs. 6.8, $n = 290$; $F = 70.4$, $P < 0.001$), but not different from those of the captive birds (adjusted $\overline{x} = 8.1$, $n = 41$, vs. 7.8, $n = 41$; $F = 0.7$, NS). Because the captive birds laid clutches similar in size to those reported from Delta, the smaller clutch size in southern Alberta appears to result from some environmental constraint. The great similarity in the relationship between clutch size and laying date in the wild in each year of the study (Fig. III-4) despite the severe drought of 1984 (Grace & Johnson 1985) and combined with Keith's (1961) clutch sizes, indicate that the breeding environment of southern Alberta is constant and apparently incapable of producing clutches equivalent to those produced in captivity or at Delta, Manitoba. Because both body reserves and food resources have been implicated as proximate determinants of clutch size in ducks (Krapu 1974, 1981, Drobney 1980, 1982), the larger clutch size of captive birds and those nesting at Delta, Manitoba could have resulted from superior quantity or quality of available food and/or superior body condition. Because there is no reason to believe that the birds breeding in Manitoba are in better condition upon arrival on the breeding ground than those nesting in southern Alberta, food resources on the breeding ground are a more plausible cause of the difference in clutch size. Whichever, it appears that food, either directly or via superior body condition, is a proximate factor influencing clutch size in Northern Pintails. Diet quality has been suggested as a proximate factor affecting clutch size in ducks (Bengston 1971, Krapu 1981) and has been shown to influence seasonal egg production in ducks (Krapu and Swanson 1975, Krapu 1979). Rowher's (1984) dismissal of food as a proximate determinant of clutch size in ducks appears unfounded. Food quality has also been shown to affect clutch size in Ruffed Grouse (*Bonasa umbellus*) (Beckerton and Middleton 1982). Similar to my results, Cowardin et al. (1985) found that the clutch size of wild Mallards in North Dakota was about 1 egg less than that produced by captive Mallards as reported by Batt and Prince (1979). In opposition to the annual consistency in clutch size that I found even during a severe drought year, Krapu et al. (1983) reported that the clutch size of Mallards averaged 0.7 egg less in a dry year.

The greatest source of variation in clutch size in the wild found in this study was the date of clutch initiation. A seasonal decline in clutch size is a feature common to many species of birds including waterfowl (Klomp 1970). The configuration of the decline in Northern Pintails, with a rapid decrease early in the season, is similar to that reported by Batt and Prince (1979) for captive Mallards but differs from that reported for wild Blue-winged Teal (*Anas discors*) (Dane 1966) and Redheads (*Aythya americana*) (Low 1945). In the latter two species, clutch size remained stable until the second half of the nesting season and then declined. In adult Northern Pintails, clutch size declined and then levelled off about midway through the season. The levelling off suggests that there may be some minimum clutch size below which it is not worth producing a clutch (Batt and Prince 1979).

My data refute a number of hypotheses that have been proposed to explain the seasonal decline in clutch size on a proximate level. The persistence of a declining clutch size in the captive birds despite ad libitum food supply discounts the proximate effect of declining food resources as the causative factor. Batt and Prince (1979) also found that clutch size of captive Mallards decreased despite unlimited food resources. The decline within the first clutches laid by captive Northern Pintails and the rapid decline in clutch size in the earliest nests in the wild negates the hypothesis that the decline may be caused by renesting birds (Davis 1955, Strohmeyer 1967, Hill 1984, Roseberry and Klimstra 1984). The seasonal decrease in clutch size by yearling Northern Pintails, both in captivity and in the wild, rejects the hypothesis that the seasonal decline results from later laying by younger birds (eg. Johnsgard 1973). A more credible explanation for the seasonal decline is that a bird's nutrient reserves decrease seasonally and that clutch size is limited by these body reserves (Krapu 1981, Hamann 1983). The idea of body reserve depletion has been most strongly supported by work on some species of arctic-nesting geese which appear to rely exclusively on endogenous reserves for clutch formation (Ryder 1970, Ankney and MacInnes 1978). In some species of ducks, body lipid reserves may be important to egg formation although protein is obtained from exogenous sources (Drobney 1980, 1982, Krapu 1981). In other birds, protein reserves appear to be important rather than lipid reserves (Jones and Ward 1976, 1979, Houston et al. 1983), while in some small passerines, reserves seem to be of little, if any, importance to egg production (Newton 1972, Perrins 1979). Murton and Westwood (1977) pointed out that anatids are unusual in their reliance on body reserves for egg production, and that in many other birds, nutrients for egg-laying are derived primarily from daily food intake. Thus, the body reserve depletion hypothesis appears an unlikely explanation for the seasonal decline of clutch size in birds other than some waterfowl. Within the waterfowl, late-nesting ducks such as Gadwall (*Anas strepera*) and Lesser Scaup exhibit a seasonally decreasing clutch size despite the fact the birds are on the breeding ground weeks prior to nesting, likely building up their reserves rather than depleting them. Consequently, the reserve depletion hypothesis lacks broad applicability as an explanation for the seasonal decline in clutch size in birds. In this study, the presence of a clutch size decline in the first nests of the individually-housed Northern Pintail pairs with ad libitum food also makes the reserve depletion hypothesis appear improbable. It has been proposed that the seasonal decline in clutch size is ultimately adaptive and is regulated proximately by a seasonal decrease in the body reserve threshold at which a bird will commence laying, such that later in a nesting season, a bird may commence laying with lower body reserves, thus producing a smaller clutch (Reynolds 1972, Drent and Daan 1980, Birkhead et al. 1983). However, this hypothesis also relies upon a direct relationship between body reserves and clutch size and as such, lacks widespread applicability.

Considering the general inappropriateness of the above hypotheses and the great similarity in clutch size among years in Northern Pintails, it would appear that laying date alone may be the proximate factor governing the seasonal decrease in clutch size (see also Koskimies 1957, Coulsen and White 1961, Batt 1979). The mechanism by which laying date exerts its influence on clutch size is unknown although daylength and temperature have been suggested (Dane 1966, Klomp 1970). Photoperiod (and a photorefractory response) would seem more plausible in view of its precise regularity, its importance in the regulation of reproductive readiness in birds (Farner and Follett 1979), and indications that it may affect clutch size in domestic fowl (*Gallus domesticus*) (Byerly and Moore 1941). The overriding influence of laying date on clutch size and the great similarity among years emphasize that laying date must be analyzed in purported annual fluctuations in clutch size as clutch size will be lower when birds nest later. For example, Bengston (1971) reported annual variation in clutch size of some duck species and attributed it to food supplies although there is no evidence that he analyzed the data for differences in laying date. In Northern Pintails, mean overall clutch size could be lower in a late year because of the influence of later mean laying date.

On an ultimate level, the laying of smaller clutches later in the season has often been considered an adaptation to declining food resources for the young, particularly in altricial species (Lack 1966, Perrins 1970, 1979, Weeks 1978). Numerous other studies have dismissed this possibility because food resources have been found to be stable or increasing later in a breeding season (von Haartmann 1971, Hussell 1972, Bryant and Westerterp 1983, Newton and Marquiss 1984). Hamann (1983) thought that the ultimate reason for the seasonal decline in clutch size in Lesser Snow Geese (*Anser caerulescens caerulescens*) might be synchronization of hatching among clutches. At the time Hamann suggested this, the idea of adaptive synchrony of hatching in snow geese was in vogue (Findlay and Cooke 1982). Since then, however, it has been illustrated that selection favors earlier-hatching clutches over synchronously-hatching clutches (Cooke et al. 1984). Another view is that the decrease in clutch size is not adaptive and is merely an artifact of some physiological process such as decreased hormonal activity (Soikkeli 1967), although Farner and Follett (1979) point out that even physiological responses such as photorefractoriness may be adaptive.

Toft et al. (1984) recently examined the seasonal decline in brood size in a number of duck species and, as here, rejected various proximate causes that had been proposed to explain this phenomenon. They proposed that the ultimate explanation for the seasonal decrease in clutch size was the increased proportion of duckling mortality occurring at fledging in late-hatched broods compared to early-hatched broods. They suggested that this increased risk after maximum reproductive investment by a hen could select for a reduced clutch size if hen survival to the next breeding season was enhanced as a result. I suggest that a more catholic, ultimate reason for reduced fecundity later in a breeding season is the widespread seasonal decrease in offspring survival rate whereby young hatched relatively late in a breeding season suffer increased mortality (see references cited above). This has been suggested as the ultimate cause of the seasonal decline in clutch size in other groups of birds (Klomp 1970, Hussell 1972, Parsons 1976) and is also dependant upon the subsequent increase of a bird's fitness. Bet-hedging theory predicts that reproductive effort will be reduced in the face of decreasing survival prospects for offspring (see Wittenberger 1981: 356 for review). Reduced breeding effort late in a breeding season might also be selected for if larger clutches are detrimental to adult survival at that time because of approaching stresses (eg. molt, migration, winter).

Yearling Northern Pintails nesting in the wild laid significantly smaller clutches than did adults. This difference persisted after the later laying dates of yearlings was accounted for. Young individuals of numerous species of ducks lay relatively small clutches (see Afton 1984 for review). A number of studies of various bird species, including some waterfowl, have shown that the smaller clutch size in younger birds does not simply result from the later laying of younger birds (Coulsen and White 1961, Perrins and Moss 1974, Baillie and Milne 1982, Rockwell et al. 1983, Afton 1984). Reduced reproductive output in young waterfowl and other birds appears to result from lack of experience rather than age per se (Lehrman and Wortis 1960, Batt and Prince 1978, Finney and Cooke 1978, Burley 1980, Aldrich and Raveling 1983, Loman 1984). The captive yearling Northern Pintails in this study had the physiological capability to lay larger clutches than did adults in the wild. Thus, the smaller clutch size of yearling Northern Pintails in the wild is not the result of some fixed ultimate "strategy". Similarly, Batt and Prince (1978) found that the captive environment negated any differences in productivity between yearling and adult Mallards. The smaller clutch size of younger birds of various species in the wild has often been attributed to a lower foraging efficiency (Klomp 1970, von Hartman 1971, Searcy 1978, Harvey et al. 1979, Baillie and Milne 1982, Roskaft et al. 1983).

The captive Northern Pintails exhibited considerable variation in clutch size despite the relative environmental constancy. Individual differences in clutch size in some species of waterfowl result from hereditary factors (Prince et al. 1970, Birkhead et al. 1983, Findlay and Cooke 1983) as in other birds (Klomp 1970, Perrins and Jones 1974, van Noordwijk et al. 1980, Flux and Flux 1982, but see Smith 1981). Thus, some of the variability apparent in the captive Northern Pintails may have been due to genetic differences. The maintenance of genetic diversity in a trait such as clutch size which is, presumably, closely related to fitness, is a genetic paradox in light of Fisher's (1930) Fundamental Theorem which predicts a disappearance of additive genetic variance (narrow heritability) because of strong selective pressure. Rose (1984) and Price and Grant (1984) pointed out, however, that genetic variance in a trait that is closely related to fitness need not mean that fitness itself has significant additive genetic variance. Strong selective pressure on precise clutch size could be precluded because of overriding influences of events which are independent of clutch size such as a high rate of total clutch loss (Ricklefs and Bloom 1977, Smith 1981, Price 1984). Environmental variability among years and resulting differences in fitness values has also been suggested as a cause of genetic polymorphism in clutch size (Lack 1948, Hilden 1964, Mountford 1973, Batt 1979, van Noordwijk et al.

1980).

The body weight of Northern Pintails was not related to clutch size. Loman(1984) reported that Hooded Crows (*Corvus corone*) that were relatively heavy had a tendency to lay larger clutches whereas Price (1984) found that reproductive effort was not related to body size in Darwin's finches. In species that rely on body reserves for egg production, such as some arctic-nesting geese, clutch size may be dependent upon weight of the bird (Ankney and MacInnes 1978).

In summary, the clutch size of Northern Pintails is affected by hen age, environmental conditions, and possibly individual variation. Food availability and foraging efficiency may be involved in the age-related and environmental differences.

The ultimate limiting factor on clutch size in precocial birds is speculative with four main hypotheses proposed: 1)limited food availability for egg production, 2)limited brood-rearing ability, 3)limited incubation capacity, and 4)increased probability of nest predation with larger clutches. Evidence and arguments have been presented that show that hypotheses 3) and 4) are unlikely explanations for clutch size in waterfowl (Winkler and Walters 1983, Rowher 1985). Recently, Rowher (1985) presented evidence that the clutch size of Blue-winged Teal is not limited by brood-rearing ability because females can successfully rear broods that are larger than normal. Although duckling survival and variance in brood survival rates did not differ among brood-size classes, the observed variance in brood success for normal- and large-sized broods was greater than expected. Theoretical evidence predicts that decreased fecundity will be selected for in the face of increased variance in offspring survival (Gillespie 1977, Wittenberger 1981: 356) and thus, although brood-rearing ability does not appear to limit clutch size, further research is warranted. Rowher (1984) conducted egg removal studies and found that birds in the wild could not be induced to lay larger clutches. He suggested that ducks in the wild lacked sufficient nutrients because captive birds with ad libitum food appeared capable of laying larger clutches and thus, the egg production ability hypothesis appeared to be supported. Rowher's (1984) conclusion in support of the egg production ability hypothesis, is contrary to evidence presented by Sowls (1955), Strohmeyer (1967), and Gates (1962), who found that ducks in the wild can, and do, lay larger clutches than normal via continuous laying. Continuous laying in the wild resulted in the production of a normal-sized clutch in the second nest despite the hen having previously laid some eggs, illustrating that ducks have the capacity to lay a larger clutch than they do. The fact that birds which exhibited continuous laying changed their nest site, whereas birds in removal experiments laid their eggs in a single nest, may involve some physiological change whereby a new nest results in an entire new clutch being laid. The production of larger-than-normal sized clutches in the wild via continuous laying is contrary to the predictions of the food limitation hypothesis and suggests that clutch size is not maximized according to food availability.

Renesting

The lack of renesting found in the radio-marked birds in 1982, the small number of birds found renesting in 1983, and the similarity of the nesting chronology in 1983 to that of 1982 despite the induced 0% nest success rate in the latter year show that renesting by Northern Pintails was uncommon on the study area. Sowls (1955) considered Northern Pintails to be the most persistent renesting duck of the five species he examined on the Delta Marsh in Manitoba. Milonski (1958) and Derrickson (1977) indicated that Northern Pintails exerted a strong renesting effort in Manitoba and North Dakota, respectively, based on nesting chronologies. Derrickson (1977) found that although Northern Pintails in North Dakota started to nest in the third week of April, the peak nest initiation was in the 2nd-4th week of May. This relatively late peak in nesting compared to that found in the present study could be indicative of a strong renesting effort: the latest clutch in my study was initiated June 23 compared to July 6 in North Dakota (Stewart 1975, cited by Derrickson 1977). Stoudt (1971) believed that Northern Pintails seldom renested at Redvers, Saskatchewan, and Smith (1971) considered Northern Pintails to be less prone to renest than Mallards or Canvasbacks (*Aythya valisineria*) at Lousana, Alberta. Keith (1961) estimated the extent of renesting in various duck species in southeastern Alberta from pair counts and number of nests, however, he omitted Northern Pintails because of their early departure from the area. This early departure of Northern Pintails also implies a low incidence of renesting. It appears that Northern Pintails are much less inclined to renest in Alberta and Saskatchewan than in Manitoba and North Dakota. This regional disparity could be related to the reduced water permanency in the more arid prairie regions of southern Alberta and Saskatchewan. Bellrose (1976) suggested that renesting in Northern Pintails may be related to the stability and availability of water areas. Other species of ducks appear to exhibit reduced renesting effort during dry years (Krapu et al. 1983, Afton 1984, Doty et al. 1984, Cowardin et al. 1985). During the 2 years when I investigated renesting in the wild, 1982 and 1983, the unadjusted number of July ponds surveyed by the Canadian Wildlife Service and United States Fish and Wildlife Service in southern Alberta (survey strata 28 and 29) was 125 and 90, respectively, compared to the 1955-1985 mean of 112 (Waterfowl Production Survey-1985, Canadian Wildlife Service). Thus, the late summer water status varied between slightly above and below the long-term mean and the results reported herein represent average conditions. Renesting might increase in a very wet year. Low renesting effort in the grasslands of Alberta and Saskatchewan might also result from poorer food resources. Food supply appears to regulate the extent of renesting in Blue-winged Teal (Swanson and Meyer 1977) and other birds species (Soikkeli 1967, Hilden 1975). Diet composition also affects overall egg production in captive ducks (Krapu and Swanson 1975, Krapu 1979). Renesting may be particularly important to the productivity of Northern Pintails breeding in cultivated areas because they readily nest on cultivated land where many first clutches are destroyed by agricultural practices (Milonski 1958, Higgins 1977, Krapu 1977).

The presence of a very small secondary peak in the nesting chronology of wild Northern Pintails during the latter half of May and the late May laying dates of the five wild renesting hens indicate that the middle of May is a reasonable, albeit somewhat subjective, date after which new nests may be attributed to renesting hens. Based on marked renesting birds and nesting chronology, Sowls (1955) considered Northern Pintail hens laying later than May 20 to be renesting hens. Milonski (1958) used May 19 in one year and June 6 in another, as the cut-off points after which he attributed new nests to renesting, based on nesting chronologies. In my study, the lack of nests produced after May 20 during 1984, a severe drought year (Grace and Johnson 1985), indicates that there was virtually no renesting in that year.

Analysis of the age structure in 1982 and 1983 showed a resurgence of laying adults relative to yearlings in late May and June, probably a result of renesting by adults. The laying of a second clutch by only half of the captive yearlings could be an indication of relatively low reproductive effort in younger birds (see Afton 1984). Because no yearlings were found nesting in the wild in the last few weeks of the nesting season, there would appear to be relatively little or no renesting by yearlings. Undoubtedly, renesting is less common in yearlings than in adults, if for no other reason than their later first nest initiations. Older Mallards renest more frequently than do yearlings in both the wild (Cowardin et al. 1985) and in semi-captive conditions (Swanson et al. 1985). The lack of experience, perhaps in foraging, that could be a cause of smaller clutches in yearlings (see above), might also cause lower renesting ability in the wild. If yearlings exhibit lower renesting persistency compared to adults despite ad libitum food, this could be indicative of an ultimate strategy for reduced reproductive effort by younger birds.

Sowls (1955) characterized renesting by the presence of a renesting interval, a period of days between loss of a clutch (or brood) and initiation of another clutch, to distinguish it from continuous laying. The renesting intervals of four of the five hens recaptured in this study were substantially longer than that reported by Sowls (1955; 63% of his data points were from Northern Pintails). The captive study showed that Northern Pintails are capable of 9-10 day renest intervals under conditions of food abundance. Ward and Batt (1973) stated that this is the average renest time for captive ducks. Swanson et al. (1985) found that the mean renest interval for semi-captive Mallards was about 7 days. The greater length of time between nest attempts in wild Northern Pintails in this study as compared to that in captivity and to Sowls (1955) could be indicative of food shortage. Swanson et al. (1985) found that food resources can affect the length of the renest interval in Mallards. Sowls (1955) reported numerous renest intervals from the wild that were less than the 9-10 days found here in captive Northern Pintails. A number of other studies on various ducks have found longer renest intervals for hens that lose their clutches early in incubation than those recorded by Sowls (eg. Grice and Rogers 1965, Hunt and Anderson 1966, Coulter and Miller 1968, Alliston 1979, Doty et al. 1984), although some captive Mallards and wild teal (*Anas discors* and *A. cyanoptera*) have been found with renest intervals less than 8 day (Hunt and Anderson 1966, Strohmeyer 1967, Prince et al. 1970, Swanson et al. 1986). The renest interval of the captive birds in this study was not related to the date on which the clutch was taken, in contrast to Alliston's (1979) findings.

The lack of any difference in renesting characteristics of hens on 14% and 29% protein diets appears somewhat contrary to that of previous studies. Krapu and Swanson (1975) reported that Northern Pintails laid fewer eggs on an 18% protein wheat and oystershell diet than on a 23% protein pelleted ration. Krapu (1979) found that Mallards on a 14% protein wheat diet produced only half as many eggs as those on a 29% protein feed (both were supplemented with ad libitum oystershell). Both of the above studies compared wheat as a low protein diet to a high protein feed and showed that grains are inferior to higher protein diets, thus demonstrating a need for invertebrates which have a higher protein content on average than plants. The lack of a difference reported herein suggests that the importance of invertebrates is not simply their high protein level relative to plant material but some other factor(s), such as their concentration of essential amino acids, vitamins, phosphorous or other constituents of animal matter (Scott et al. 1969). Although Holm and Scott (1954) recommended a minimum of 18.6% protein for breeding ducks, I found that 14% was adequate. Their recommendation was based on the results of an "unsatisfactory" 17% protein diet which appeared to result in lower hatchability but did not alter egg production. Hatchability was not examined in the present study. As in most dietary studies, Holm and Scott's (1954) two diets were not comparable in all other aspects and consequently, attributing possible reduced hatchability to lower protein level could be premature. Another possible complicating factor in nutritional studies of ducks is that some researchers have examined continuous egg production by collecting eggs daily (eg. Holm and Scott 1954, Krapu and Swanson 1975) as opposed to examining clutch size as done here.

Only 50% of all females in captivity renested despite ad libitum high quality food. In the wild, 35 % of the birds radio-tagged in 1982 apparently left the study area soon after their first nesting attempt failed. Derrickson (1977) also found that some Northern Pintail hens left the breeding area immediately after their nests were destroyed. Studies on other duck species have reported birds leaving an area after only one nesting attempt and it has been suggested that there may be individual variation in renesting persistency (Coulter and Miller 1968, Humberg et al. 1978). The absence of renesting in half of the captive birds herein could reflect a proportion of hens that would not renest in the wild, irrespective of environmental conditions.

Although Sowls (1955) considered the Northern Pintail to be the most persistent renesting species of the ducks he studied, he was unable to get a good estimate of Mallard renesting effort for comparison. Because Mallards appear to renest repeatedly in the prairie pothole region (Swanson et al. 1985), and their nesting season is often longer than that of Northern Pintails (Miller and Collins 1954, Milonski 1958), they are likely more persistent renesters. The northern migration of Northern Pintails which has been reported in drought years (Smith 1970, Derksen and Eldridge

1980) might be a reflection of the lack of renesting persistence in the Northern Pintail relative to other early-nesting ducks. Because Northern Pintails nest around shallow waterbodies which are more ephemeral and susceptible to drought than parkland waterbodies, the breeding habitat is less stable and the renesting effort of Northern Pintails may be relatively low on average.

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IV. VARIATION IN EGG SIZE OF THE NORTHERN PINTAIL

INTRODUCTION

The size and/or number of offspring produced by an animal must be compromised if reproductive output is limited by availability of some resource. The ultimate reason for the size of egg in a given species presumably represents some optimal trade-off between egg size and clutch size (Smith and Fretwell 1974), which is determined by factors such as the level of competition, predation, and environmental uncertainty (Wilbur 1977). Larger eggs could improve a neonate's probability of survival because young may hatch in a more advanced state of development or with greater body reserves (Klomp 1970). Larger offspring could also have an advantage because they are competitively superior, have the ability to use a broader resource base, and are less vulnerable to predators (Reznick 1982). In some species, larger young have faster growth rates than smaller young (Schifferli 1973, O'Connor 1975), but not in others (Ricklefs 1977, Furness 1983). The primary factor limiting the size of eggs and young may be the theoretical trade-off between egg size and clutch size. Additional selective forces opposing larger eggs could be the selective advantage of breeding early when there is less food, restrictions on large body size of the adult female with a positive correlation between egg size and body size, energetic constraints of incubation and brood-rearing, and food availability (Lundberg and Vaisanen 1979).

Egg size is positively correlated with offspring survival in some bird species, particularly larids (Furness 1983, Ojanen 1983, and references therein). The results of many of these studies may not be germane to a discussion of optimal egg size however because they examined intra-clutch rather than inter-clutch variation and showed that chicks from the smaller, last eggs may have lower survival. A number of other studies have found no effect of egg size on offspring mortality and have questioned the importance of egg size to overall reproductive success (Davis 1975, Brooke 1978, Barrett and Runde 1980). Egg size could be more important to the survival of offspring in altricial species than in precocial species (Vaisanen et al. 1972).

In comparison with other birds, waterfowl lay unusually large eggs relative to their body size (Murton and Westwood 1977). In ducks, as in other taxa of birds, larger species have a smaller egg size/body size ratio than do smaller species (Lack 1967). Lack (1967) and Ryder (1970) speculated that larger eggs are advantageous in waterfowl because they increase offspring survival by producing larger young which have larger fat reserves for surviving temporary food shortages. Larger waterfowl neonates can survive longer without food than smaller conspecifics (Krapu 1979, Ankney 1980). Rhymer (1982) found that larger ducklings are also more energy efficient at maintaining homeothermy but have reduced growth rates and fledge at the same age as smaller ducklings. Unlike other reproductive characters, egg size and weight are reported to have a high heritability, similar to morphological features (van Noordwijk et al. 1981, Moss and Watson 1982, Ricklefs 1983). The heritability of a trait measures the additive genetic proportion of the total variation within a trait and may have implications regarding the importance of the trait to fitness (Falconer 1960). Because Fisher's (1930) fundamental theorem predicts the disappearance of additive genetic variance (narrow heritability) in traits closely related to fitness, the preservation of a large heritable component in egg size may mean that it is relatively unimportant to overall fitness or that genetic variability has been maintained as a result of environmental heterogeneity (Moss and Watson 1982).

Proximate factors known to affect egg size in various species of birds are female age (Preston 1958, Davis 1975, Brooke 1978, Furness 1983, Thomas 1983), female body size (Festing and Nordskog 1967, Vaisanen 1977, Grant 1982, Loman 1984), laying date (Coulson et al. 1969, Parsons 1972, Runde and Barrett 1981, Furness 1983), and diet (Krapu 1979, Sharp and Moss 1981, Beckerton and Middleton 1982).

This paper examines the variation in egg size of Northern Pintails breeding in southern Alberta and the causes of that variation. The effect of a number of factors including hen age, clutch number, environment, and diet were investigated. Individual consistency and the heritability of egg size under changing environmental conditions were also examined.

STUDY AREA AND METHODS

The study of the wild population was conducted in an area of grazed mixed grass prairie (Coupland 1961) about 35 km south-east of Brooks, Alberta between 1983 and 1984. The study area included four impoundments which are managed for waterfowl production by Ducks Unlimited Canada. These were described by Giroux (1981; impoundments D, E, F and G).

Searches for nests on the artificial islands were conducted by walking across them systematically at least once every 3 weeks. On the mainland, nests were located by dragging a 50-80 m steel rope between two vehicles along parallel transects. Duck nests were attributed to a species based on observation of the flushing hen, and occasionally by characteristics of the eggs and feathers in the nest. To obtain data on individuals, Northern Pintail hens were trapped on their nests using drop traps (Sowls 1949), modified Weller traps (Weller 1957), or bow-net traps (Sayler 1962). Hens were identified as either yearlings or adults based on wing-feather characteristics (Duncan 1985). All hens were weighed, their tarsometatarsus measured, and were banded to identify renesting individuals.

Egg length and breadth were measured at the longest and widest points with vernier calipers and an index of egg size was calculated by length x breadth^2. Eggs that were not incubated were weighed on a pan balance. The stage of incubation of eggs was estimated by candling the eggs and using Weller's (1956) guide to embryo development. Laying date was calculated by back-dating from the stage of incubation and the number of eggs in the clutch. For analyses of clutch size, only incubated clutches were used; those which had been parasitized or exhibited signs of partial clutch depredation were not used.

To examine egg size under controlled conditions, Northern Pintails were hatched from eggs taken from the study area in 1983 and reared in captivity at the Brooks Wildlife Center of the Alberta Department of Energy and Natural Resources. Eggs were marked and the ducklings web-tagged to identify them as being from a particular clutch. When pipped, eggs were transferred to a hatching incubator where the ducklings remained until weighed at 24 ± 4 h after hatch. This was done to determine the relationship between hatch weight and egg size.

The birds were raised in captivity, wing-clipped to prevent flight, and maintained on an ad libitum commercial waterfowl maintenance diet until the spring of 1984. They were exposed to natural daylength but had access to relatively warm indoor facilities during the winter. Forty-one pairs of birds, most of which had paired naturally, were placed into individual 4.6 x 9.2 m pens between March 26-April 2, 1984 where they were essentially visually isolated. The ground within the pens was sparsely vegetated in early spring. Secluded nest-sites were provided. Each pen contained a water basin (46 x 33 x 12 cm) in which the water was changed daily. Half of the pens also had 220 x 230 cm cement ponds which sloped to maximum depth of 20 cm. The water in these ponds was changed infrequently, allowing stagnation and dense algal growth. Penned pairs were initially maintained on a 29% protein commercial waterfowl diet provided ad libitum (Shur-Gain Div., Canada Packers Inc.). Crushed oystershell was also provided ad libitum throughout the study. All clutches produced were removed on the third day of incubation. When the first clutches were taken, every second pair was put onto a diet of 14% protein commercial feed (Shur-Gain Div., Canada Packers Inc.). All birds were removed on June 28-29 after nesting activity had ceased. Hens were weighed and their tarsometatarsi and culmens measured immediately before and after being confined in the breeding pens.

For the analyses of clutch size of captive birds, I used only incubated clutches in which all eggs were laid within a single nest bowl; clutches in which eggs were "dropped" during laying or within 7 days of clutch initiation were not included. This eliminated potential error when abnormally large "clutches", which may have resulted from continuous laying, are included. Continuous laying occurs when birds are disrupted during the laying sequence, desert their nests, but continue to deposit eggs in a new nest without a break in the laying cycle (ie. no change in laying interval; Sowls 1955).

As there was no difference in egg size between years, data from both years was combined for the various analyses. Statistical analyses were performed using the SPSSX package. The significance level was set at alpha = 0.05; values greater than this are considered not significant (NS). Where means are presented, they are followed by the standard error. Heritability was examined through regression analysis of egg size of daughters against those of their mothers and repeatability through analysis of variance using the within and between component variances (Falconer 1960).

RESULTS AND DISCUSSION

The volume index used herein (length x breadth^2) was strongly correlated with the fresh weight of the egg ($r = 0.95$, $n = 93$, $P < 0.00001$), and thus was a good indicator of egg size. This index has also been found to be a good indicator of the mass or volume of eggs in other species (eg. Birkhead and Nettleship 1981, van Noordwijk et al. 1981, Murphy 1983). The volume index was also closely related to the weight of the day-old duckling ($r = 0.94$, $n = 60$, $P < 0.00001$). Similarly, egg size has been found to be proportional to hatchling size in numerous other birds (Howe 1976, Lundberg and Vaisanen 1979, Bancroft 1984 and references therein).

The mean volume index of eggs from Northern Pintail clutches in the wild was 73.9 ± 0.4 cm^3 [Fig. IV-1; n (clutches) = 166]. Using the volume index-egg weight

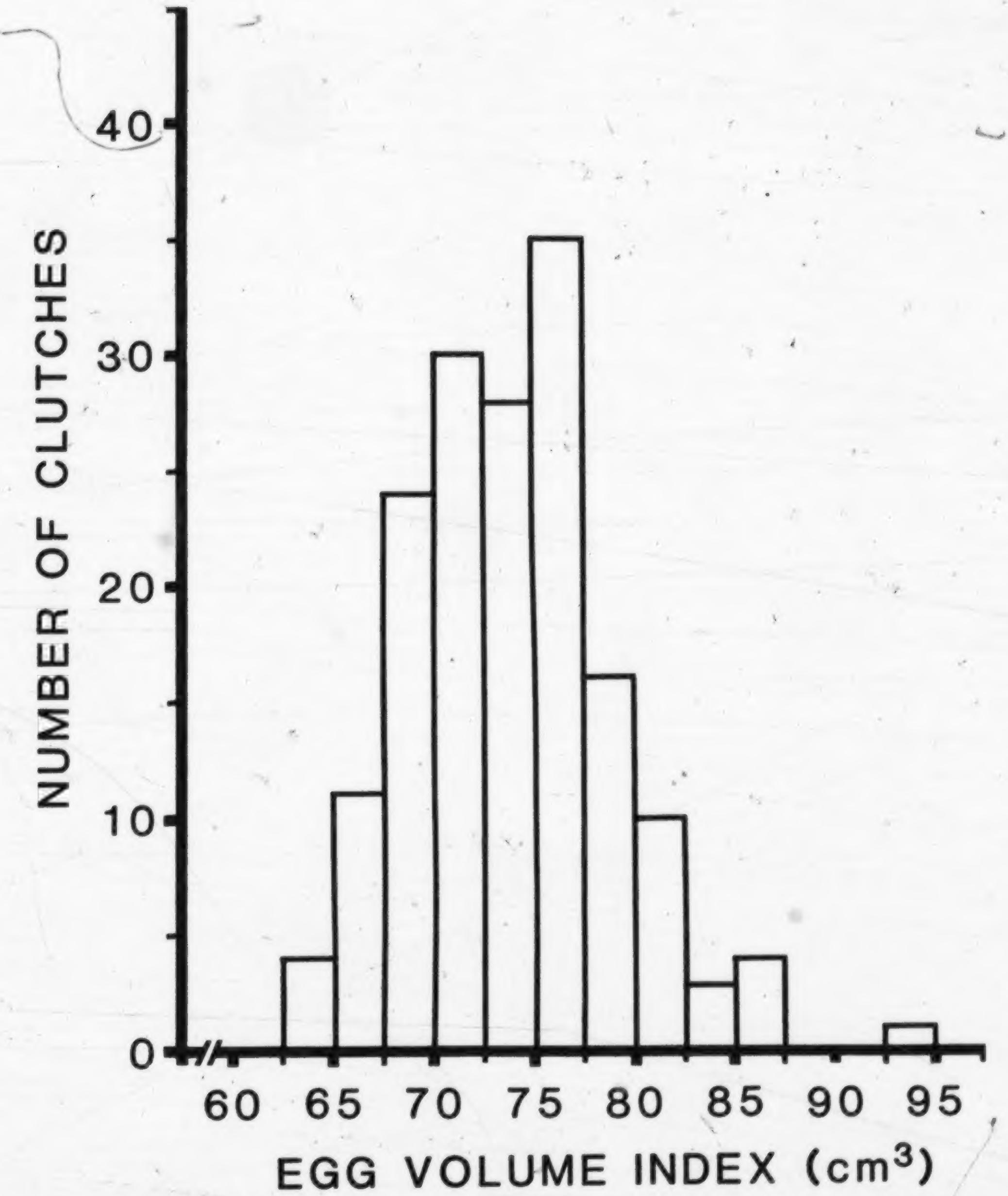

Fig.IV-1. Frequency distribution of mean egg volume index (length x breadth2) of Northern Pintail clutches from southern Alberta.

regression, the corresponding mean weight of fresh wild Northern Pintail eggs was 40.3 g. To compare the egg size with those reported from other studies of Northern Pintails, I calculated the mean length and breadth using all eggs; these produced a mean volume index of 73.7 cm^3, which was lower than the 76.6, 78.2 and 77.1 cm^3 indices calculated from data in Fuller (1953), Bellrose (1976), and Palmer (1976), respectively.

The mean egg size of clutches was not related to laying date in the wild ($r = 0.083$, $n = 168$, NS), nor in captivity ($r = 0.003$, $n = 64$, NS). Hill (1984) found that there was a seasonal decline in the egg volume of tufted ducks (*Aythya fuligula*) but not in Mallards (*Anas platyrhynchos*). In many species of sea-birds, egg size decreases progressively with later laying dates (Runde and Barrett 1981 and references therein).

Yearling and adult Northern Pintails did not lay different sized eggs in the wild (yearlings: 72.6 ± 0.9 cm^3, $n = 31$; adults: 74.0 ± 0.5 cm^3, $n = 105$; $t = 1.34$, NS). Batt and Prince (1978) found that the mean egg weights of captive yearling and adult Mallards were also similar. Younger birds lay smaller eggs in a number of species including American Coots (*Fulica americana*) (Crawford 1980), Semipalmated Sandpipers (*Calidris pusilla*) (Gratto et al. 1983), and many species of seabirds (Brooke 1978, Thomas 1983, and references therein). Although this age effect has been suggested as a factor in the observed seasonal decline in egg size in some species (see above) because younger birds lay later (Runde and Barrett 1981, Hill 1984), a seasonal decline that is independent of age has been found in some species (Coulson et al. 1969, Lloyd 1979).

The weight of an incubating wild Northern Pintail hen showed a weak positive correlation with her mean egg size ($r = 0.34$, $n = 124$, $P < 0.0001$), however, the mean egg size of first clutches from captive birds was not related to the hens' pre-breeding or post-breeding weights ($r = 0.04$, -0.15, respectively, $n = 39$, NS). The largest mean egg volume index found in the wild (94.5 cm^3, Fig. IV-1), was produced by a hen that weighed 820 g, > 80 g more than the next heaviest bird. Without this individual, the correlation was even weaker ($r = 0.24$, $P < 0.005$). The relationship between egg size and hen weight may reflect a slight tendency for bigger birds to lay bigger eggs as suggested by a trend between tarsometatarsus length and egg size in wild hens ($r = 0.16$, $n = 124$, $0.10 > P > 0.05$), and culmen length and egg size in the captive birds ($r = 0.21$, $n = 39$, $0.10 > P > 0.05$). Batt and Prince (1978) found that egg weight was not related to hen weight in captive Mallards, similar to the situation in captive Northern Pintails. Female body size or mass has a small, positive effect on egg size in domestic chickens (*Gallus domesticus*) (Festing and Nordskog 1967), shorebirds (Vaisanen 1977, Ross 1979, Nol et al. 1984, Ricklefs 1984), and a few other species (eg. Grant 1982, Loman 1984).

Comparing various species of anatids, Lack (1967, 1968) found a general inverse correlation between clutch size and size of the egg relative to body size. He argued that this relationship reflected a broad trade-off between egg size and food availability. However, the validity of comparing birds of greatly different size from different tribes or subfamilies is questionable (see Stearns 1983,1984) and does not bear directly on the possible existence of an intraspecific relationship. Although theory predicts a trade-off between number and size of offspring (Smith and Fretwell 1974), proximate evidence for such a relationship is sparse. The clutch size of wild and captive Northern Pintails was not correlated with egg size (r = 0.08, *n* = 168; r = 0.13, *n* = 42; respectively, NS). Hill (1984) also failed to find a correlation between clutch size and egg size in Mallards and Tufted Ducks. No relationship has been found between these parameters in a number of other bird species (Bryant 1975, Moss et al. 1981, Birkhead et al. 1983), although an inverse relationship does exist in poultry egg production (Marks 1981) and a few wild species of birds (Manning 1978, Ojanen et al. 1978). Bezzel and Schwazenbach (1968, cited by Murton and Westwood 1977) reported a positive correlation between clutch size and egg length (but not breadth) in ducks. In contrast, Koskimies (1957) found a trend towards an inverse relationship between clutch size and egg length in Velvet Scoters (*Melanitta fusca*). The clutch size of Northern Pintails was related to neither mean length nor breadth of eggs from wild birds birds (r = -0.12, r = 0.05, respectively, *n* = 124, NS), nor those from the first nests of captive birds (r = -0.08, r = -0.14, *n* = 39, respectively, NS).

The mean egg size of second clutches was larger than that of first clutches for captive Northern Pintail hens maintained on a consistent diet of 29% protein, whereas the egg size of birds given a 14% protein diet during renesting decreased but not significantly (Table IV-1). Five hens which were found renesting in the wild laid similar sized eggs in each attempt (1st nest, 77.4 ± 2.3 cm^3; 2nd nest, = 77.0 ± 2.3 cm^3; paired *t* = 0.58, NS). Batt and Prince (1979) found that captive Mallards laid slightly but significantly heavier eggs in their second and third clutches although the egg weight in the first and fourth clutches did not differ. They suggested that there might be an adaptive trade-off whereby egg size is increased in later clutches to offset the seasonal reduction in clutch size that occurs. However, the lack of a difference between the weight of eggs in their first and fourth clutches, and the inequity between the increase in mass via larger eggs (1-2 g/egg) and the decrease in mass via reduced clutch size (50 g/egg), appear to argue against substantial ecologically-adaptive value to this phenomenon. Egg size increases between first and renest clutches in some other birds (Ojanen et al. 1979, Parker 1981), whereas in others it decreases (Runde and Barrett 1981, Nol et al. 1984).

Table IV-1. Effect of diets with differing protein content on mean egg size (length x breadth^2) of renest clutches of Northern Pintails.

Dietary protein (1st/2nd clutch)	*n*	Egg size ($\bar{x}$ ± SE cm^3) 1st clutch	Egg size ($\bar{x}$ ± SE cm^3) 2nd clutch	Difference[a]
29%/14%	10	82.8 ± 1.9	79.6 ± 2.8	NS
29%/29%	9	83.3 ± 1.7	86.4 ± 1.5	*
Difference[b]		NS	*	

[a] Paired *t*-test; * = $P < 0.05$, NS = $P > 0.05$.

[b] Independant *t*-test.

Diet affected the egg size of Northern Pintails. Although egg size was similar in the first clutches of 2 groups of birds on a 29% protein diet, birds that renested with that diet layed significantly larger eggs in their second clutches whereas those switched to a 14% protein diet for renesting layed somewhat smaller eggs, such that the egg size of second clutches differed between the 2 groups (Table IV-2). In addition, the mean egg size of first clutches of captive daughters was greater than that of their wild mothers (81.6 ± 1.1 vs. 75.1 ± 0.7 cm^3, $n = 24$, paired $t = 5.38$, $P < 0.001$), possibly a result of the ad libitum, high quality diet. Mallards on a wheat (14% protein) diet supplemented with oystershell laid lighter eggs than birds on a 29% protein feed (Krapu 1979). Grouse also lay smaller eggs on lower protein diets (Sharp and Moss 1981, Beckerton and Middleton 1982). Attributing differences in egg size to a specific dietary factor is not possible because the diets vary not only in protein but also in amino acid composition and other parameters. Nevertheless, there are indications that animal protein and perhaps methionine level may affect egg size (Krapu 1979, Sharp and Moss 1981).

Lack (1968) thought that the variation in egg size of some penguins, in which the smallest egg was 58% of the weight of the largest, was unusually high. Similarly, Ankney and Bissett (1976) found that the smallest egg in Lesser Snow Geese (*Anser caerulescens c.*) was 59% of the weight of the largest, and proposed that annual variation in environmental conditions in the arctic maintained this large egg size heterogeneity. The egg size of Northern Pintails also differed substantially among clutches; the volume index of the smallest viable egg was 56% of the largest in the wild and 55% in captivity. Thus, the amount of variation in Northern Pintail eggs is as great as that in the above-mentioned species which have been considered aberrant. More appropriate measures of variation are the ratios of smallest to largest mean egg size per clutch rather than of individual eggs to eliminate the effect of abnormal eggs, or preferably, coefficients of variation (C.V.) which standardize for different sample sizes. Although the amount of variation in the size of Northern Pintail eggs appears considerable, it is less than or equal to that which exists in a number of other morphological parameters (Table IV-2). For a valid comparison, the C.V.'s of egg volume indices should be compared to body mass whereas the C.V.'s of egg measurements (lengths and breadths) should be compared to other linear measurements (Simpson et al. 1960). Because the variability in egg size is of the same magnitude as those that exist in other parameters, it would seem to merely represent the overall variation inherent in a wild population. Thus, a specific hypothesis to explain egg size variation (eg. Ankney and Bissett 1976) may not be necessary. As in other species (Preston 1958, Montevecchi et al. 1983, Lundberg and Vaisanen 1979), egg breadth in Northern Pintails is less variable than egg length. It might

Table IV-2. Variation in a number of parameters of wild and captive Northern Pintails from southern Alberta.

Parameter	Mean ± S.E.	*n*	C.V.[a]	Smallest/ largest(%)
WILD				
Egg volume index (cm^3)	73.8 ± 0.4	166	0.07	67.4
Hen weight;incubating (g)	612 ± 7	133	0.09	64.6
Egg length (mm)	52.7 ± 0.1	166	0.03	83.1
Egg breadth (mm)	37.4 ± 0.1	166	0.02	88.6
Hen tarsus (mm)	49.1 ± 0.1	133	0.03	87.4
CAPTIVE				
Egg volume index (cm^3)[b]	82.5 ± 0.8	40	0.06	80.7
Hen weight;pre-breeding (g)	720 ± 9	42	0.08	71.1
Hen weight;post-breeding (g)	701 ± 12	42	0.11	66.3
Egg length (mm)[b]	54.5 ± 0.3	40	0.03	87.7
Egg breadth (mm)[b]	38.9 ± 0.2	40	0.02	91.4
Hen tarsus (mm)	50.5 ± 0.2	46	0.03	88.4
Hen culmen (mm)	47.2 ± 0.3	46	0.04	80.0

[a] Coefficient of variation (S.D./mean).

[b] Using clutch means from first clutches.

be expected that egg size in captivity would be less variable than that in the wild because of the relatively homogeneous conditions for all captive birds. This was not the case, however, as the mean egg size of the first clutches of the captive daughters was more variable (C.V. = 0.06, n = 24, range 74.7-92.6 cm^3) than that of their wild mothers (C.V. = 0.04, n = 15, range 69.6-80.5 cm^3). The increase in variability in egg size among females under more homogeneous environmental conditions suggests that there is substantial inherent differences between individuals which was moderated in the natural environment.

Individual Northern Pintails hens had a tendency to lay eggs of the same size. The repeatability value (a measure of individual consistency with values between 0 and 1) for mean egg size of the captive birds between first and second clutches was 0.61 (n = 19), showing that hens had a moderately high tendency to lay eggs of the same size. The birds on the 29% protein diet had a slightly higher repeatability than those switched to a 14% protein diet (0.66, n = 9, vs. 0.56, n = 10, respectively). A small number of hens that were recaptured in the wild had an even higher repeatability in egg size (within years = 0.87, n = 5; between years = 0.84, n = 5). Captive Mallards have an egg weight repeatability of 0.62 (Batt and Prince 1978), and captive Canvasbacks (*Aythya valisineria*) have an egg size repeatability of 0.58 (Kostow and Bluhm 1984). Egg sizes of other species of birds have moderate to high repeatabilities between years (van Noordwijk et al. 1980, 1981, Moss and Watson 1982, Nol et al. 1984). Within numerous other bird species, a major part of the variation in egg size is attributable to differences between nests (may include > 1 nest/individual) or females (Vaisanen et al. 1972, Ojanen et al. 1979, Furness 1983, Bancroft 1984, Birkhead and Nettleship 1984, Ricklefs 1984). Thus, a large part of the variation in egg size of birds, including Northern Pintails, results from differences between individuals.

Because repeatability values indicate the amount of variation between individuals relative to the total phenotypic variance (Falconer 1960), and because the variation between individuals can be both environmental and genetic, repeatabilities set an upper limit to the possible importance of heritable factors as a cause of variation. Although a high repeatability is sometimes used to infer a strong genetic effect, it does not necessarily follow because environmental effects may be important. For example, Smith (1981) found significant repeatabilities in 3 measures of reproductive performance but no significant heritabilities. The heritability value of egg size of Northern Pintails was examined by comparing the mean egg size of first clutches of captive daughters to the egg size of their wild mothers. The regression for all daughter-mother combinations was not significant ($r^2 = 0.01$, $n = 24$, NS), but, because a number of daughters were sisters and thus not independent, a regression of the combined mean egg size of all daughters on that of their mother was also conducted but was also insignificant ($r^2 = 0.03$, $n = 15$, NS). Thus, there was no significant relationship between the egg size of daughters and that of their mothers and thus no heritability value could be calculated. Although the mean egg size of the captive daughters was larger than that of their wild mothers (see above), the lack of a significant heritability value shows that all genotypes were not equally affected. Prince et al. (1970) found that in captivity, the egg weight of Mallards had a heritability of 0.55, but Kostow and Bluhm (1984) found that the value for captive Canvasbacks was only 0.19. A significant genetic effect on egg size has been found in Mute Swans (*Cygnus olor*) (Birkhead et al. 1983), and egg size is moderately to highly "heritable" in chickens (King and Henderson 1954, Festing and Nordskog 1967, van Tijen and Kuit 1970), and Great Tits (*Parus major*) (Ojanen et al. 1979, van Noordwijk et al. 1980,1981). Because heritability values are the proportion of variance due to additive genetic factors relative to total variance (Falconer 1960), an increase in environmental variance increases the total variance and thus decreases the heritability value, just as the reduction of environmental variation (ie. captive conditions) can increase it (Merrel 1981, Falconer 1960). The lack of a significant heritability value for egg size in Northern Pintails could be caused by increased environmental variance resulting from the comparison of birds in the wild to those in captivity. If the egg size of Northern Pintails does have a significant genetic component that was obscured because of the alteration in environmental conditions, there must have been a genotype-environment interaction because each genotype was not equally affected. Assuming there is some heritable component to egg size in Northern Pintails, this study illustrates the lability of egg size and the potential effect of environmental conditions of the magnitude encountered in this study to differentially alter egg size. In opposition to the results reported herein, Moss and Watson (1982) found that the egg size of Red Grouse (*Lagopus lagopus scoticus*) had a heritability value of 0.66 between wild mothers and captive daughters, despite the change in environments. Their finding could reflect a relatively stronger genetic effect on egg size or may have resulted from comparatively little environmental variance between wild and captive conditions relative to this study.

Heritability values are dependent upon, and therefore restricted to, the population and environment studied (Falconer 1960, Merrell 1981, Berven and Gill 1983). Their usage is fraught with problems such as maternal effects which may artificially inflate the heritability of egg size (King and Henderson 1954, Vaccaro and Van Vleck 1972) and genotype-environment interactions and correlations (Lerner 1972, Merrel 1981, Smith and Zach 1979). Consequently, heritabilities are useful primarily for the purpose for which they were designed--as an index of response to selective breeding, not as a measure of the importance of the genotype to phenotype (Feldman and Lewontin 1975), which is generally of greater interest to ecologists. This is reflected by the fact that heritability values from a parent-offspring regression are estimated from the regression coefficient (slope of the regression line) and not the correlation coefficient (strength of the relationship).

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V. BODY RESERVES OF NEONATE NORTHERN PINTAILS

INTRODUCTION

Newly-hatched nidifugous birds must maintain themselves by catabolism of body reserves until they have begun feeding at a suitable feeding site and are able to sustain themselves by foraging. Ducklings generally remain in the nest for 12-24 h after hatching and do not feed until their second day of life or later (Kear 1965, Bjarvall 1968). During this time, a duckling is believed to sustain itself by assimilating the contents of its yolk sac and body fat deposits (Kear 1965, Marcstrom 1966). Although little is known of the composition and function of the yolk sac in newly-hatched birds, yolk reserves are generally thought to be extremely important as a source of food and energy for newly-hatched birds (Romanoff 1944, Freeman 1971, Skutch 1976), and that mortality of young may be related to the size of their yolk reserves (Notini 1945 cited by Siivonen 1952, Coulson et al. 1969, Parsons 1970).

This study examines the body reserves in the carcass, yolk sac, and liver of neonate Northern Pintails (*Anas acuta*). The hypothesis that the yolk sac is the source of food and energy for neonates is tested and the importance of the various body reserves to the growth and survivability of the ducklings is investigated.

METHODS

The study was conducted during 1983-1984 using ducklings hatched from eggs that were laid in the wild near Brooks, Alberta, and in captivity by birds held in captivity at the Brooks Wildlife Center of the Alberta Department of Energy and Natural Resources. The captive birds were reared from eggs taken from the wild in 1983. Some eggs were incubated naturally until pipped, whereas others were artificially incubated at a dry bulb temperature of 37.5°C and a wet bulb temperature of 31.1°C. When eggs were pipped, they were transferred to a hatching incubator with a dry bulb temperature of 36.9°C and wet bulb temperature of 33.6°C. Ducklings were kept in the hatcher for 12-24 h before being transferred to brooding facilities with heat lamps and free access to water.

To examine the use of body reserves in the absence of food, unfed ducklings were sacrificed at 0, 12, 24, 48, 72, and 96 h after hatch. Ducklings and their yolk sacs and livers were weighed, and all components were then frozen for subsequent lipid analysis. Lipid extractions were conducted using petroleum ether in a Soxhlet apparatus.

To determine the importance of the yolk sac, deutectomies (yolk sac removals) were performed between 0-1 h after hatch following the procedure outlined by Rinaudo et al. (1982). Lido-2 was used as an anesthetic. Sham-operated ducklings were anesthetized, incised, and a small portion of their yolk sac was extruded and replaced, before being sutured. Growth of deutectomised and sham-operated ducklings was monitored by weighing ducklings and measuring their culmens and tarsometatarsi with vernier calipers at 1 day of age and subsequent 2 day intervals up to 11 days of age. The culmen was measured between the distal tip and the proximal median of the upper mandible. Measurement of the tarsometatarsus included the distal condyle of the tibiotarsus. Ducklings were fed 22% protein goose and duck starter (Lakeside Feeders Ltd.) ad libitum. The life-span of a small number of unfed deutectomised and sham-operated ducklings of other species was measured to determine the importance of the yolk sac under starvation conditions. A few ducklings were also placed in a refrigerator and their temperature was monitored periodically by sliding a thermistor probe down the esophagus into the proventriculus.

Statistical analyses were conducted using the SPSSX package with a significance level of 0.05. Non-significant results are indicated by NS and means are followed by standard errors. The terms neonate and newly-hatched refer to ducklings 0-1 h old, and carcass refers to the duckling without feathers, bill, feet, yolk sac, and liver.

RESULTS AND DISCUSSION

Ducklings

Northern Pintail ducklings decreased in weight between hatch and 4 days of age in the absence of food (Table V-1, r

Table V-1. Fresh weight (g) of food-deprived Northern Pintail ducklings, their yolk sacs, and livers as a function of age (mean ± SE).

Age	*n*	Duckling[a]	Yolk sac	Liver
Hatch	16[b]	29.7 ± 1.2	2.33 ± 0.12	0.67 ± 0.02
12 h	3	28.8 ± 1.9	1.89 ± 0.10	0.93 ± 0.13
24 h	4	25.7 ± 1.0	0.66 ± 0.11	1.02 ± 0.07
48 h	5	26.2 ± 1.0	0.14 ± 0.08	1.14 ± 0.08
72 h	4	26.0 ± 0.3		0.98 ± 0.11
96 h	4	22.2 ± 1.9		0.88 ± 0.15

[a] Including yolk sac and liver.

[b] *n* = 6 for livers.

= -0.56, *n* = 33, P < 0.0005). The correlation may have been weakened by: 1) the considerable variation in duckling size (Duncan 1986) and small sample sizes, and 2) the fact that individuals were not weighed repeatedly.

Neonate Northern Pintails have a very high fat content. Lipids comprised 43% of the dry mass of newly-hatched Northern Pintails (excluding feathers, bill and feet) (Table V-2). This was more than the 35% found in Lesser Scaup (*Athya affinis*) (Sugden and Harris 1972).

The lipid index (g lipid/ g lean dry mass) of neonate Northern Pintails was 0.74, higher than the 0.44-0.57 values calculated for Mallards (*Anas platyrhynchos*) (Ricklefs 1977, Rhymer 1982), and the 0.30 index found in Wood Ducks (*Aix sponsa*) (Clay et al. 1979). Although Ricklefs (1977) calculated a lipid index of 0.75 for chickens (*Gallus domesticus*) from Medway and Kare's (1957) data, I recalculated it as 0.54, similar to the 0.40-0.50 values from Romanoff's (1932, 1967) data. All these values are high compared to the 0.10-0.40 indices from neonates of various other bird species including numerous altricial species (Ricklefs 1967, 1977, Brisbin 1969, Brisbin and Tally 1973, Dunn 1975, Dunn and Brisbin 1980, Bryant and Hails 1983). It appears that altricial birds [and Japanese Quail (*Coturnix coturnix japonica*)] hatch with relatively low fat content and then increase their lipid levels as they grow (Ricklefs 1967, Clay et al. 1979). The higher fat content of precocial neonates can be related to the initial composition of eggs;

Table V-2. Lipid and lean mass (g) of carcass, yolk sac, and liver of food-deprived Northern Pintail ducklings as a function of age (mean ± SE).

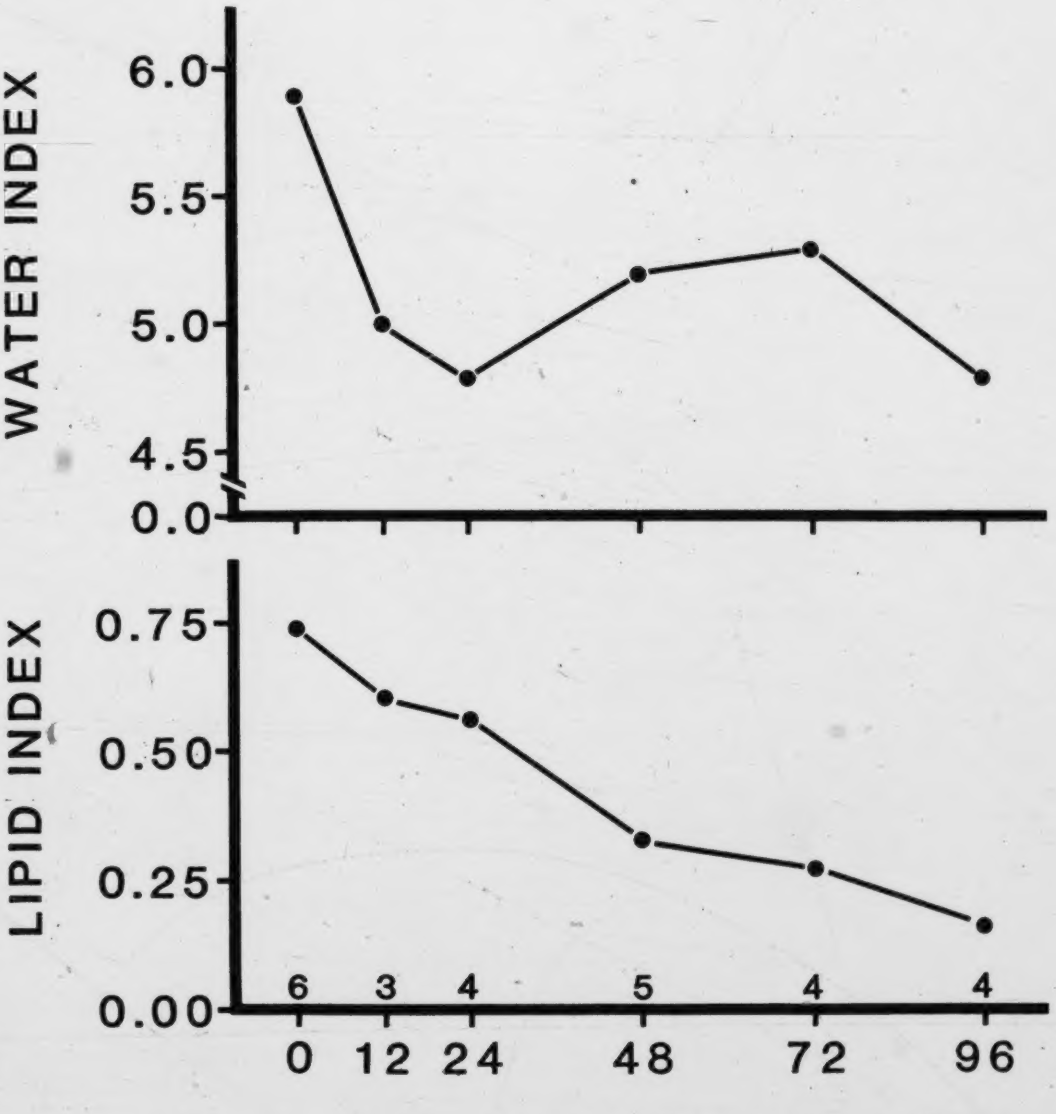
		Carcass[a]		Yolk sac		Liver	
Age	*n*	Lipid	Lean	Lipid	Lean	Lipid	Lean
Hatch	6	2.13 ± 0.15	3.26 ± 0.08	0.71 ± 0.08	0.56 ± 0.07	0.11 ± 0.01	0.13 ± 0.00
12 h	3	1.93 ± 0.26	3.63 ± 0.24	0.57 ± 0.05	0.52 ± 0.04	0.11 ± 0.01	0.18 ± 0.03
24 h	4	1.88 ± 0.14	3.55 ± 0.15	0.20 ± 0.04	0.15 ± 0.02	0.12 ± 0.01	0.20 ± 0.01
48 h	5	1.19 ± 0.16	3.83 ± 0.14			0.10 ± 0.01	0.22 ± 0.01
72 h	4	0.96 ± 0.14	3.79 ± 0.07			0.10 ± 0.03	0.18 ± 0.02
96 h	4	0.48 ± 0.15	3.53 ± 0.26			0.11 ± 0.04	0.22 ± 0.06

[a] Excluding feathers, bill, feet, yolk sac, and liver.

fresh eggs of precocial birds generally contain a greater proportion of lipid-rich yolk than do eggs of altricial species (Carey et al. 1980, Ricklefs 1977). The ultimate reason(s) for this relationship could be higher post-embryonic energy demand, and/or higher incubation energy demand because of longer incubation periods for eggs of precocial species (Ricklefs 1977).

The lipid index of food-deprived Northern Pintail ducklings dropped from 0.74 to 0.16 by 4 days after hatch (Fig. V-1). At fat indices less than 0.20-0.30, lipids can be used only with a concurrent catabolism of non-fat tissue (Odum et al. 1964, Johnston 1968), and consequently critical body tissues begin to deteriorate. Newly-hatched Northern Pintail ducklings are able to survive 4-5 days after hatch without food (unpubl. data, Krapu 1974). By 5 days of age, Northern Pintail ducklings will have used up virtually all their lipid reserve (Fig. V-1). Mallard ducklings, which are larger than Northern Pintail ducklings, can survive 5-7.5 days (Marcstrom 1966, Krapu 1979). Within a species, large waterfowl young survive starvation longer than smaller ones (Krapu 1979, Ankney 1980).

The water index of Northern Pintails was higher than that reported from other ducks. The water index (g water/ g lean dry mass) of Northern Pintail ducklings dropped in the first 12 h after hatch, likely a result of dehydration and drying of their plumage while in the hatching incubator, and then fluctuated between 4.8-5.3 (Fig. V-1). The water index



AGE OF DUCKLING (h)

Fig.V-1. Changes in water index (g water/g lean dry mass) and lipid index (g lipid/g lean dry mass) of food-deprived Northern Pintail ducklings (minus feathers, bill, and feet) after hatch. Sample sizes are above x-axis.

of newly-hatched Mallards is 2.7-3.3 (Ricklefs 1977, Rhymer 1982) and that of Wood Ducks is 2.4 (Clay et al. 1979). Chickens have a water index of 4.7-5.4 (Medway and Kare 1957, Romanoff 1967). The water indices of various other neonate birds, including numerous altricial species, ranges from 3.0-7.5 (Ricklefs 1967, 1977, Brisbin 1969, Brisbin and Tally 1973, Dunn and Brisbin 1980, Ricklefs and White 1981, Bryant and Hails 1983). Ar and Yom-Tov (1978) speculated that the higher water content found in fresh eggs of altricial species compared to precocial species is to provide altricial young with more water because they are fed dry food. Although altricial young often have a higher water content than precocial young (Ricklefs 1967, 1983, Dunn 1975, Dunn and Brisbin 1980), the value found here for Northern Pintails and other data (Ricklefs 1977) show that the relationship between developmental type and water content is indistinct. Clay et al. (1979) thought that young waterfowl may hydrate during their early growth whereas altricial birds and Japanese Quail dehydrate at this time.

Carcass

The carcass of neonate Northern Pintails contains a large amount of fat with lipids comprising 40% of the dry mass at hatching (Table V-2). This is higher than the 35% found in Mallard ducklings (Marcstrom 1966), and the 28% found in Capercaillie (*Tetrao urogallus*) chicks (Marcstrom 1960). Fats comprise about 23% of the dry weight of chicken embryo carcasses near hatching (Romanoff 1932). The lipid index of carcasses of newly-hatched Northern Pintails was 0.65, higher than the 0.44 value found in Mallard carcasses (Ricklefs 1977). The indices for carcasses of another precocial species and a semi-precocial species were 0.36 and 0.26, respectively, whereas that of 2 altricial species was 0.16 and 0.29 (Ricklefs 1977). Thus, it appears that ducks may hatch with relatively large carcass fat stores compared to other birds and that precocial young may tend to have more carcass fat than altricial young. Although I did not look for body fat deposits specifically, I did notice sizeable fat depots on the legs of neonate Northern Pintails. Subcutaneous fat deposits have been reported from the bodies of Mallard ducklings (Kear 1965, Marcstrom 1966). Newly-hatched chickens have specific fat depots on their bodies (Liebelt and Eastlick 1954) although Freeman (1971) stated that chickens, unlike some birds, have little subcutaneous fat with most of their adipose tissue being intra-abdominal.

The carcass fats of a newly-hatched Northern Pintail duckling comprise 72% of the neonate's total lipid reserves, higher than the 60% that Ricklefs (1977) found in 2 Mallard ducklings. Lipids in neonate galliform carcasses comprise less of the total lipid reserve; about 50% in Capercaillie chicks (Marcstrom 1960) and chickens (Romanoff 1932). Theberge and West (1973) stated that Rock Ptarmigan chicks (*Lagopus mutus*) had little subcutaneous fat and that body fats were not an important energy source. On the contrary, Ricklefs (1977) concluded from Marcstrom's (1960, 1966) studies that more of a neonate's energy reserves are in its body fat than in its yolk sac although he maintained that yolk was an important energy source for neonates.

The lipid mass in the carcass of unfed Northern Pintail ducklings decreased with time after hatch (Table V-2, $r = -0.88$, $n = 27$, $P < 0.00001$). Greater than 75% of the neonate's carcass lipids were used to sustain the duckling up until 4 days of age. The lipids in Northern Pintail carcasses decreased from 40% of the dry weight (lipid index = 0.65) to only 12% (lipid index = 0.14) by 4 days after hatch (Fig. V-2). The body fats in the carcasses of starved Mallard ducklings decreased from 35% at hatch to 11% ~~at~~ 7 days of age (near death) (Marcstrom 1966) and that of Capercaillie chicks fell from 28% to 11% by 5 days after hatch (near death) (Marcstrom 1960). Thus, neonate Northern Pintails catabolize their substantial carcass fat deposits to survive in the absence of food. Lipids are known to be the main source of energy in newly-hatched chickens (Freeman 1971).

There was a small increase in carcass lean mass after hatch (Table V-2, $r = 0.35$, $n = 27$, $P < 0.05$), primarily attributable to an increase during the first 12 h after hatch. Because no food was eaten, the increase in lean mass must come from the yolk. Marcstrom (1960, 1966) found that the dry weight of Capercaillie chicks and Mallard ducklings

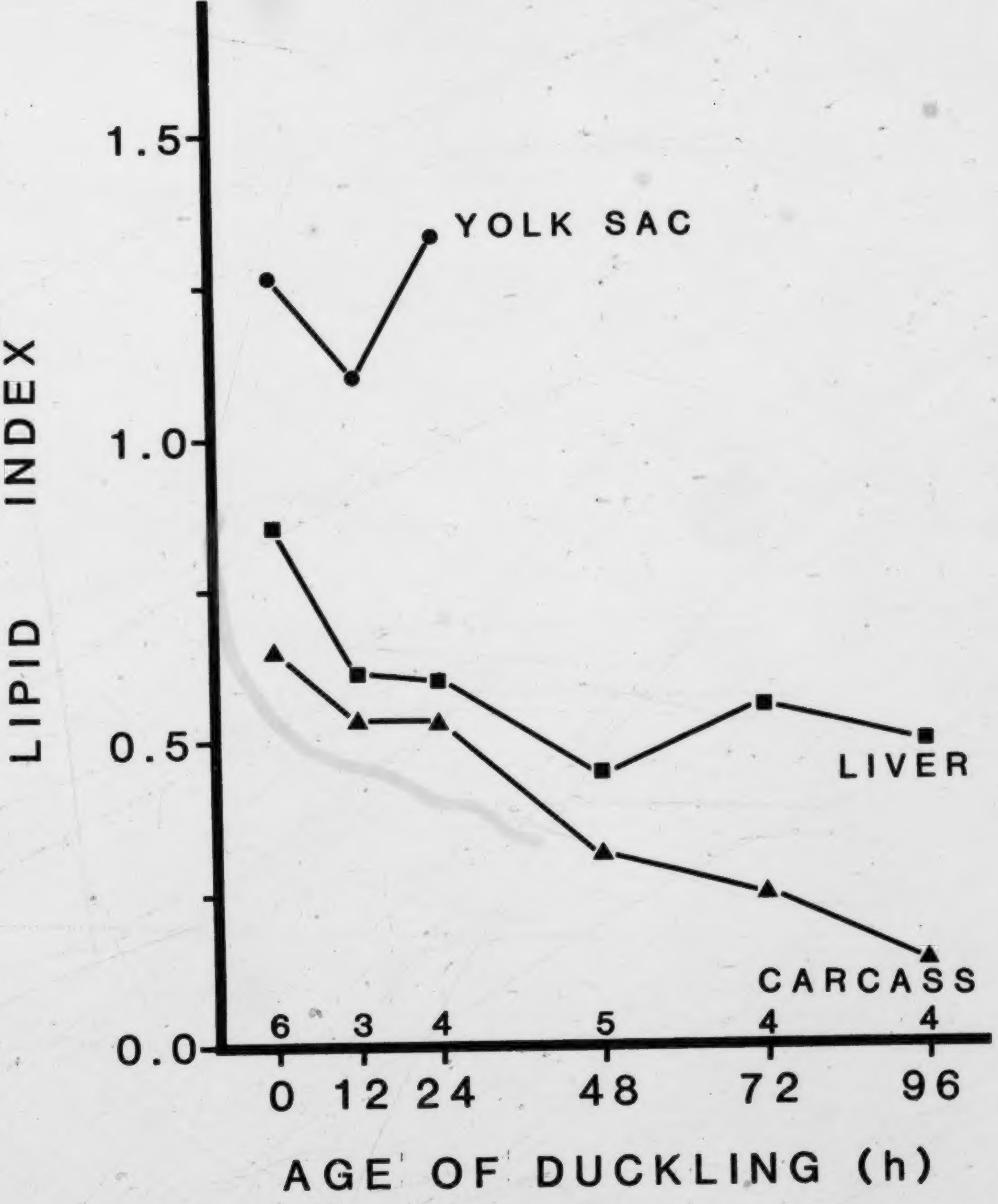


Fig.V-2. Change in lipid index (g lipid/g lean dry mass) of yolk sac, liver, and carcass of food-deprived Northern Pintail ducklings after hatch. Sample sizes are above x-axis.

increased in the first 1-2 days of life, caused by an increase in the non-lipid fraction. Ricklefs (1977) also noted that during hatch and the change from reliance upon body reserves to food supply, the growth rate of precocial chicks did not slow.

Yolk Sac

The mean weight of yolk sacs from newly-hatched Northern Pintails was 2.3 ± 0.1 g (*n* = 16). The average weight of these ducklings at hatching was 29.7 ± 1.2 g so that the yolk sac comprised 8% of their body weight. The yolk sacs of 4 neonate Gadwalls (*Anas strepera*) and 3 Lesser Scaup (*Aythya affinis*) that I examined were 9% and 10% of their body weights respectively. Yolk sacs also constitute 9-14% of the weight of newly-hatched Mallards (Kear 1965, Marcstrom 1966) and 9% in Tufted Ducks (*Aythya fuligula*) (Kear 1970). Yolk reserve comprises 11% of the body weight of neonate Japanese Quail but is 18% of the body mass of Laughing Gulls (*Larus atricilla*) (Ricklefs et al. 1978) and 17% in Capercaillie (Marcstrom 1960). The yolk sac of various domesticated and semi-domesticated birds also appears to be quite large, comprising 9-19% of the neonate's mass at hatching with a trend towards relatively larger yolk sacs in birds laying larger eggs (Romanoff 1944). Although it is often suggested that precocial young hatch with a relatively greater proportion of yolk reserve compared to altricial young (Blem 1976, Ar and Yom-Tov 1978, Carey

1983), the relationship is not clear-cut if it exists at all (see also Ricklefs 1974). The average proportion in ducks is more similar to the 8% found in altricial species than the 15% found in other precocial species (Vleck et al. 1980).

The yolk sacs of Northern Pintails atrophy with time after hatch (Table V-1, $r = -0.90$, $n = 28$, $P < 0.00001$). The yolk reserve is almost completely gone by 48 h after hatch with relatively little being used during the first 12 h after hatch. Most of the yolk sac of Mallard ducklings is also assimilated in the first 2 days after hatch (Kear 1965, Marcstrom 1966) as is that of Double-crested Cormorants (*Phalacrocorax auritus*) (Dunn 1975). The yolk sacs of gallinaceous birds, which appear to be relatively larger than those of ducks, persist for a somewhat longer time (Marcstrom 1960, Bergerud 1970). The yolk sacs of numerous domesticated and semi-domesticated birds appear to persist longer than those of wild birds with substantial yolk left at 4 days after hatch (Romanoff 1967). Kear (1965, 1970) speculated that food reserves from the yolk sacs of ducklings are transferred to the liver and subcutaneous body fats after hatching. Rinaudo et al. (1982) showed that some of the amino acids and fatty acids of the yolk sac are used to create hepatic glycogen after hatch. It is presumed that proteinaceous materials from the yolk sac are used by the neonate for tissue synthesis (Marcstrom 1960, 1966) and growth (Bancroft 1985). The non-lipid fraction of the yolk is nearly all protein (Romanoff 1967, Green 1980), and it would appear that this material contributes to the increase of lean carcass tissue after hatch (see above). Some yolk materials enter directly into the blood stream of the neonate from the highly-vascularized yolk sac (Romanoff 1944, Rinaudo et al. 1982). In addition, some yolk materials may enter directly into the small intestine through the yolk stalk that connects the yolk sac to the intestine (Marcstrom 1960, Romanoff 1960), although others believe it does not (Freeman and Vince 1974).

The lipid content of the yolk sacs of newly-hatched Northern Pintails averaged 56% of its dry weight (Table V-2), higher than that reported from other species. Ricklefs (1977) found that lipids constituted 51% of the dry weight of 2 yolk sacs from neonate Mallards and the proportion varied between 39-52% in a number of other species (Marcstrom 1960, Ricklefs 1977, Ricklefs et al. 1978). Fat constitutes 33% of the dry weight of chicken yolk sacs at hatching (Romanoff 1967). The lipid index of 1.3 in the yolk sac of newly-hatched Northern Pintails (Fig.V-2) was also greater than the 0.7-1.1 indices found in a number of other species (Marcstrom 1960, Ricklefs 1977).

Lipids constitute a lower proportion of the dry mass of yolk sacs than they do of fresh egg yolks (Ricklefs 1977, Williams et al. 1982). The lipid content of 4 yolks from fresh Northern Pintail eggs was 63% of their dry weight compared to 56% in the yolk sac. The relative amounts of various yolk constituents changes during incubation (Saito et al. 1965), including a decrease in the proportion of lipid (Budowski et al. 1961, Noble and Moore 1967).

At hatching, the yolk sac of Northern Pintails contains 24% of the total lipid in the duckling (Table V-2). Although the lipid index of the yolk sac is higher than that of the carcass (Fig. V-2), the larger mass of the carcass meant that the majority of lipid reserves are in the carcass. Studies of other species have found that the yolk sac contains a greater proportion of the neonate's total lipid reserves than it does in Northern Pintails; yolk lipids constituted 40% of all lipids in 2 hatchling Mallards (Ricklefs 1977) and about half of the energy reserves of newly-hatched Boat-tailed Grackles (*Quiscalus major*) (Bancroft 1985). The lipid index of Northern Pintail yolk sacs remained fairly constant, fluctuating between 1.1-1.3 during the 24 h after hatch when most of its contents were being assimilated (Fig. V-2 and Table V-1). Romanoff (1967: 200) found that the lipid of chicken yolk sacs was absorbed at only a slightly greater rate than was protein.

To appraise the value of the yolk sac as an endogenous food source against starvation, deutectomies were conducted on a small number of ducklings and the survivability of these birds was determined in the absence of food. Four Gadwall ducklings without yolk sacs survived a mean of 125 h (range 116-142 h) while three that were sham-operated lived an average of 130 h (range 117-139 h). Three Lesser Scaup ducklings that were deutectomised lived for an average of

122 h (range 117-125 h) while two sham-operated neonates lived 117 and 135 h. This demonstrates unequivocally that the contents of the yolk sac of newly-hatched ducklings are not an important food source for the maintenance of ducklings during starvation. Romanoff (1944) believed that the domestic birds he studied relied upon their yolk sacs during starvation. In opposition to this common belief, Marcstrom (1960) doubted that the size of the yolk sac in newly-hatched Capercaillie chicks was important to their ability to tolerate starvation and later (Marcstrom 1966) concluded that body lipids were the most important energy source during starvation for both Mallard ducklings and Capercaillie chicks. In addition, Kear (1965) thought that the yolk sac might not be important to the survival of Mallard neonates because starvation did not accelerate the disappearance of their yolk reserve. In fact, the yolk sacs of birds appear to be assimilated faster in fed neonates than in starved ones (Heywang and Jull 1930, Romanoff 1944, Marcstrom 1960). Because yolk materials contain digestive enzymes (Rol'nik 1970), the intake of food might stimulate the release of some of these materials and thus hasten the assimilation of yolk. It might also be adaptive to maintain yolk material in its relatively inert state rather than convert it to energy-demanding, metabolically active tissue when there is a food shortage.

The importance of the yolk sac to the growth of Northern Pintail ducklings was also evaluated using deutectomised birds. The absence of a yolk sac resulted in lower weights, and smaller culmens and tarsometatarsi up to 11 days of age when the experiment was concluded (Fig. V-3). The differences were not due to an initial difference in duckling size as the pre-operative weights of deutectomised and sham-operated ducklings were the same (29.7, n = 9, vs. 29.8, n = 9, t = 0.03, NS) although the tarsometatarsi of the sham-operated ducklings tended to be larger ($0.10 > P > 0.05$). The appearance of a difference in culmen length at 3 days of age and the apparent increase in the difference in weight and tarsometatarsi with age show the importance of the yolk sac to growth. Because 2-2.5 week old male Mallards are larger than females (Rhymer 1982), I examined the sex ratio of the 2 groups to check for unequal sex ratios. The ratios were similar in both groups: males/females = 0.4 in deutectomised and 0.5 in sham-operated group. Freeman (1971) concluded that the absence of a yolk sac in neonate chickens does not impair their growth rate although Sloan et al. (1934) showed that yolk sacs counteract vitamin deficiencies and promote higher growth rates in poults. Barott et al. (1936) also found that deutectomised neonate chickens have lower metabolic rates. The function of the yolk sac in the growth of ducklings may be more complex than a simple contribution of proteinaceous tissue-building material because the absolute differences in weight between deutectomised and sham-operated ducklings appeared to increase with age (Fig. V-3). The yolk sac could affect

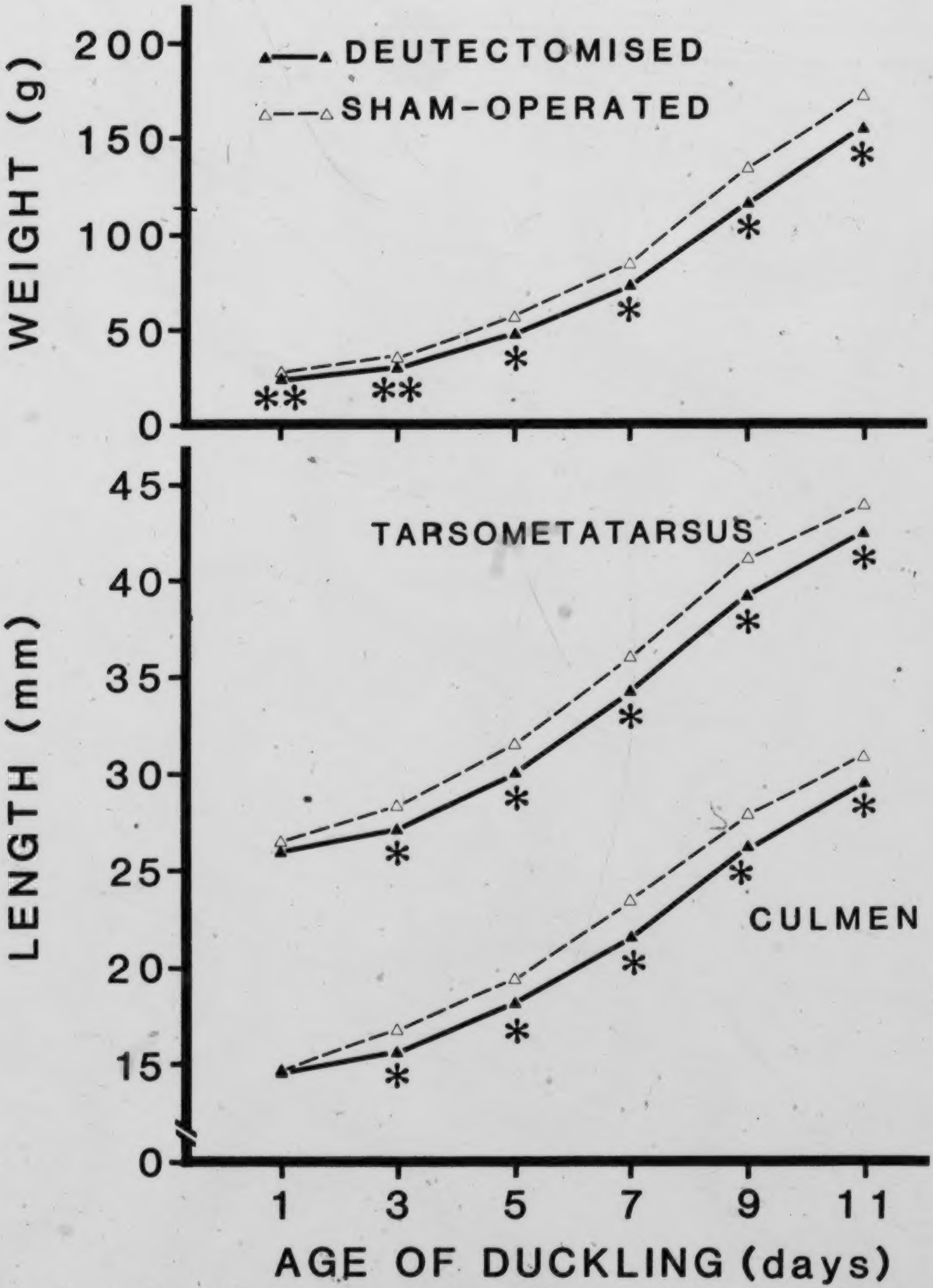


Fig.V-3. Growth of deutectomised (n=10) and sham-operated (n=9) Northern Pintail ducklings. * $P < 0.05$, ** $P < 0.005$; two-way anova with random brood effect.

growth in various ways as it has a variety of functions including digestion and anabolism, and is involved with the endocrine and lymphatic systems (Romanoff 1960, Rol'nik 1970, Freeman and Vince 1974).

Yolk sacs may also be important for the development of homeothermy in newly-hatched birds (Ar and Yom-Tov 1978). In this regard, it is interesting to note that after 4.5 h at 4°C, two 24-h-old sham-operated Northern Pintails maintained their core temperature at 41.0°C and 40.0°C respectively, whereas the temperature of 1 deutectomised duckling had dropped to 38.5°C while another had to be removed after its temperature fell to 30.0°C in only 2.5 h. Freeman (1965a) thought that the replacement of metabolically inactive yolk by actively metabolizing tissue might account for the increase in body temperature of newly-hatched chicks. Freeman (1965b) also suggested that liver glycogen stores might be involved in the maintenance of body temperature and recently, it has been shown that the yolk sac contributes synthetic materials for hepatic gluconeogenesis (Rinaudo et al. 1982).

Liver

The mass of the liver changed between hatch and 96 h after hatch (Table V-1, F = 3.65, P < 0.05), increasing in size during the first 24 h after hatch and then decreasing after 48 h. Marcstrom (1960, 1966) noted the same trend in starved Capercaillie chicks and Mallard ducklings. Kear

(1965, 1970) noted the coincidental increase in liver size and decrease in yolk reserve in neonate ducklings, and speculated that the enlargement of the liver was caused by a transfer of materials from the yolk sac. Rinaudo et al. (1982) showed that fatty acids and amino acids from the yolk sac are used to produce hepatic glycogen but the increase in glycogen that they measured is not of sufficient magnitude to account for the increase in liver size.

The livers of newly-hatched birds have a high fat content (Entenmann et al. 1940, Marcstrom 1966). The proportion of the dry weight of neonate Northern Pintail livers that was lipid was 46% (Table V-1). Marcstrom (1960, 1966) found values of 53% and 58% from Capercaillie and Mallards, respectively. The lipid index of Northern Pintail liver is higher than that of the carcass but lower than that of the yolk sac (Fig. V-2). The lipid mass of the liver remained constant throughout the 4 days after hatch (Table V-2, F = 0.21, NS). However, the lean dry mass of the liver changed with age of the duckling (Table V-2, F = 2.75, P < 0.05), primarily attributable to an increase in the first 12 h after hatch. Because the lean dry mass of the liver increased after hatch, the relative lipid content decreased (Fig. V-2). Entenmann et al. (1940) noted a decrease in the proportion of lipid in the liver of neonate chickens at 3 days of age. Marcstrom (1966) found a substantial increase and then subsequent decrease in the absolute lipid content of the liver in starved Mallard ducklings while the proportion of lipid in the dry weight remained fairly constant from hatch to 7.5 days of age.

CONCLUSIONS

Newly-hatched Northern Pintails have a high fat content relative to that of other birds. This results from the large fat reserves in their carcasses although their yolk sacs also contain somewhat more lipid than other birds. Other birds appear to have less body fat and consequently their yolk sacs comprise a higher proportion of their total lipid supply. Under starvation conditions, neonate Northern Pintails survive by catabolizing their carcass fat. The yolk sac is not an important source of endogenous nutriment in the absence of food but is important to the growth of ducklings. Yolk appears to contribute materials for the synthesis of non-fat tissue and may also act to maintain the body temperature of the newly-hatched bird and to help to establish homeothermy.

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VI. CONCLUDING DISCUSSION

Some Management Implications

The information in this study shows that the Northern Pintail is not as fecund an animal as previously believed because it has a low clutch size compared to other ducks and does not appear to be a persistent renester. The low reproductive output of the Northern Pintail relative to other ducks, particularly the Mallard, could make it more vulnerable to over-harvest. There are, however, other factors which may help to sustain Northern Pintail populations: 1) they are early migrants and thus may incur relatively low hunting mortality, and 2) the hatching success of their nests would appear to be relatively high. The preservation of large tracts of arid grassland for grazing likely maintains predation rates on Northern Pintail nests at a low level compared to the parklands where duck nests are concentrated in the small strips of remaining cover that have not been cultivated and through which predators can efficiently search. Northern Pintails do not lack upland nesting cover because much of their primary nesting habitat is grazing land and still constitutes good nesting habitat. Thus, management efforts on the breeding grounds to enhance their populations should concentrate on the provision of suitable waterbodies.

The substantial numbers of Northern Pintail nests found at distances of 1-3 km from water necessitate that subsequent surveys for duck nests in areas where Northern Pintails are fairly abundant be conducted to a much greater distance from water than typically done. Nest placement at these distances from water show that Northern Pintail ducklings commonly walk considerable distance overland. Knowing that they have this mobility on land, shallow impoundments could be created within 1-2 km of more permanent brood-rearing ponds and when the water in the ephemeral impoundments decreased, the broods could move to the permanent waterbodies. Such a system may be attractive to managers of grazing land in arid areas as the ephemeral impoundments could enhance cattle forage and may increase the grazing capacity.

Fecundity of the Northern Pintail

From previous studies, the Northern Pintail seemed to be a fairly prolific species, comparable to other dabbling ducks. Sowls' (1955) classic study of renesting in ducks on the Delta Marsh gave the impression that Northern Pintails were very persistent renesters. Bellrose (1976) reported a mean clutch size of 7.8 for Northern Pintails, summarized from various studies. Although not exceptionally small compared to other duck species, this figure is in fact lower than that recorded for any other dabbling duck and many diving ducks (see Bellrose 1976). My study shows that on the prairies of southern Alberta, Northern Pintails lay an even smaller clutch on average ($\bar{x}$ = 6.9) than indicated by

Bellrose (1976) and do not renest quickly or persistently. Thus, the evidence presented herein indicates that Northern Pintails have a lower fecundity than other dabbling ducks. The average reproductive output of Northern Pintails may be even lower than that depicted in this study because many birds appear to forgo breeding during prairie droughts (Smith 1970, Calverley and Boag 1977, Derksen and Eldridge 1980). Because droughts are more common and severe on the arid prairie grasslands where most Northern Pintails nest (Vermeer 1972, Bellrose 1979) than in the parkland where most other species of nesting dabbling ducks are concentrated, years of low overall productivity are probably more common in Northern Pintail populations. This study was conducted within the prairie region of southern Alberta where breeding Northern Pintails occur in highest densities, and thus is more representative of "typical" Northern Pintail productivity than is Sowls' (1955) study from Delta, Manitoba.

In this dissertation, I have shown that Northern Pintails breeding on the prairies of southern Alberta: 1) produce smaller clutches than birds nesting near Delta, Manitoba, 2) appear to renest less frequently than those at Delta, and 3) appear to lay smaller eggs than previously reported. I have also shown that the birds nesting in Alberta have the potential to produce larger clutches and eggs, and to renest more frequently and more rapidly when on a high quality ad libitum diet in captivity. This evidence suggests that food is limiting each of these parameters on the breeding grounds in southern Alberta. Previously, I suggested that duck brood survival is also relatively low on the grasslands of southern Alberta, and that one possible reason might be low productivity in terms of food and/or cover (Duncan 1985). One explanation that could account for the overall low productivity of Northern Pintails nesting on the grasslands of southern Alberta is that food quality and/or quantity is comparatively low.

Possible causes of this suggested nutritional limitation on reproductive output are speculative. The low amount of precipitation that falls throughout the grassland region and that is ultimately responsible for the predominance of grasses, is also reflected in a comparatively low organic content in the soils. Reduced soil nutrients might result in low overall habitat productivity including food for ducks. Relatively poor food resources for ducks on the prairies compared to other areas might also be caused by greater evaporation on the prairies, increasing the concentration of minerals at the soil surface and in shallow waters. This could have an adverse effect on the quality or quantity of food resources available to ducks. Because breeding female ducks feed primarily on aquatic invertebrates (eg. Krapu 1974, Swanson et al. 1979, 1985), as do ducklings (Sugden 1973), the above hypothesis predicts reduced availability, quantity, and/or quality of aquatic invertebrates in waterbodies in the grasslands of southern

Alberta compared to that of Delta, Manitoba.

The relatively low reproductive output of Northern Pintails breeding the the prairie grasslands appears to be paradoxical because Northern Pintails breed most densely in this region. Why would individuals breed in an area where their reproductive output appears lower (ie. southern Alberta) than in an area where their output seems higher (ie. Delta, Manitoba)? If reproductive output and ultimately fitness is greater for birds nesting in one area than another, then selection will favor those birds nesting in the "high quality" habitat. All other things being equal, these areas should come to be favored and inhabited by more individuals and the breeding population should be densest there. There would be selection for those birds "choosing' this type of habitat if the behavior has some genetic basis or there could be increased recruitment because of the greater number of young produced combined with subsequent homing to their natal area. This apparent paradox is based on the seemingly low reproductive output of birds nesting on the prairie grasslands. However, there is one important aspect of annual reproductive success that was not investigated--hatching success of nests. It appeared that the success rate on the prairie may be higher than that recently reported from intensively-farmed areas (see Oetting and Dixon 1975). Intuitively, the probability of a predator finding a nest on a large tract of prairie would seem to be relatively low. It is also quite conceivable that Striped

Skunks (*Mephitis mephitis*) are considerably less numerous on the mixed prairie than in the parklands. In Manitoba and North Dakota, many Northern Pintails nest on cultivated land where their clutches are destroyed by agricultural activity. Thus, nest success may be substantially higher on the grasslands than in cultivated areas and average reproductive output could be greater for individuals in the former habitat.

It is also possible that seasonal reproductive output is higher at Delta, Manitoba, but that lifetime reproductive output is higher for birds nesting in southern Alberta. Higher hen survival or post-fledging survival of ducklings from southern Alberta could result in higher fitness for birds nesting there. The paradox is dependent upon all other factors such as migration, wintering ground conditions, and ultimately survival being equal for birds nesting in the two areas.

The apparent paradox might also be attributable to a localized site effect. Because the clutch size I found was similar to that reported by Keith (1961), and the renesting effort on my area is in agreement with the observations of Smith (1971) and Stoudt (1971), if an anomalous area effect exists, it is more likely that Delta, Manitoba is a patch of "high quality" habitat. It might also be possible that there is a localized high density of Northern Pintails on the Delta Marsh but there is no evidence of this.

Finally, a higher density of individuals in poorer habitat may not be as paradoxical as it appears. The paradox is based on the assumption that breeding density is positively associated with reproductive output (J. Addicott, pers. comm.). However, the process(es) that regulate density may be completely independent of those that affect reproductive output and there may be no relationship between these two parameters. The seeming paradox also assumes that individuals have the freedom to choose between habitats and that they could choose to nest at Delta, Manitoba if they desired. However, young female ducks tend to return to their rearing area to breed (eg. Sowls 1955). The paradox requires that individuals have the freedom and necessary information to recognize "high quality" habitat. Although we do not know if any of these assumptions are true, the Northern Pintail possesses two behavioral attributes that would appear to make it less likely to be found inhabiting low quality breeding habitat in high numbers: 1) they pioneer new habitats readily (Hochbaum and Bossenmaier 1972), and 2) they are non-territorial and thus do not force conspecifics into poor habitats (Smith 1968, Derrickson 1978, Titman and Seymour 1981). Consequently it would seem unlikely that Northern Pintails would not find and use a patch of "high quality" habitat. It is also possible that fairly recent man-induced changes have altered the environment such that the Northern Pintail is no longer "in tune" with its breeding environment as it once was.

Yet another possibility is that clutch size is inversely desity-dependent such that a concentration of birds results in a lower clutch size. This phenomenon has been reported from a few altricial species but does not appear to be widespread and has not been found in precocial species (von Haartman 1971, Johnsgard 1973).

Female Body Reserves versus Food Resources

At the present time, there are various studies examining the importance of body reserves and/or food resources on the reproductive success of waterfowl. It appears likely that both these nutrient sources contribute in many species. The questions to be asked are what proportions and what constituents come from each of these sources. Currently there is considerable attention being given to the importance of wintering habitat conditions. Such studies are often rationalized on the basis that body condition of spring migrating ducks may be related to winter habitat conditions and ultimately may affect reproductive output. In Chapters III and IV, I suggested that food resources have a significant effect on reproductive output. Because ducks can renest in 9-10 days, it appears that the capacity exists to acquire all nutrients for egg production solely from food resources on the breeding ground. Thus, body condition upon arrival on the breeding grounds may not be as important as thought. There is a need for more study of the condition of ducks upon spring arrival on the breeding grounds and of the contribution of body reserves and food resources to reproductive success. It would be interesting to provide supplementary food to a population of ducks breeding in the wild, especially Northern Pintails in southern Alberta, to test the food limitation hypothesis.

Seasonal Decline in Clutch Size

The seasonal decline in clutch size of various avian species should be examined to test the hypotheses suggested for the proximate and ultimate causation as outlined in Chapter III. A controlled experiment that manipulated photoperiod and/or a situation in which birds were maintained in "prime" body condition but prevented from laying until late in the breeding season could test the proximate hypotheses. In terms of investigating the ultimate cause, it would be of interest to examine the existence and shape of the seasonal decline in various species of birds along with the extent and timing of mortality of adults and young. If there appears to be an adaptive, ultimate cause as suggested herein, it is conceivable that this determinant is also a very important selective factor on the initial clutch size. This could provide great insight into the evolution of clutch size in general and thus, examination of this phenomenon could be very helpful in comprehending one of the most fundamental units of fitness. For students of this phenomenon, and of waterfowl, an interesting starting point might be the examination of the proximate causes of the differing configuration of the decline in different species of ducks (see Chapter III). It is also of interest to note that there is often a seasonal decrease in egg size for those species that lay only a single egg or have small clutches and that this decline in reproductive effort might also be caused by the same ultimate factor as suggested here for decreasing clutch size.

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